

ON CENTRAL AUSTRALIAN MAMMALS
(With notice of related species from adjacent tracts)

PART III—THE POTOROINAE

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INTRODUCTION

Since the Horn Expedition of 1894 (Spencer, 1896) comparatively little has been published on the marsupials of Central Australia. This venture while rich in new discoveries, left many gaps in the detailed knowledge of eremian species. Much is still obscure regarding their general biology and local and regional distribution and status, and in particular, the level of subspecific differentiation attained by eremian marsupials in relation to corresponding forms in the peripheral areas of the continent, is almost unknown.

Pastoral settlement in Central Australia since 1894 has had an adverse effect on the mammalian life of large areas, including that worked over by the Horn Expedition, but the creation of Aboriginal Reserves originally totalling 75,000 square miles on the adjoining borders of the States of South and Western Australia and Central Australia has incidentally provided a partial sanctuary for fauna. Here the introduction of domestic stock and most other European enterprise is banned, and nearly virgin conditions prevailed until the entry of the European fox in numbers within the last 25 years.

During the years 1931-35 the writer visited this area four times spending in all some 13 months in field observation and collecting, between $136^{\circ} 30'$ and $128^{\circ} 10'$ East and $23^{\circ} 30'$ and $28^{\circ} 0'$ South (approx.). The main collecting stations and routes covered during this portion of the work are indicated upon a detailed map which accompanies a general description of the country, published by the writer in 1936 and two preliminary papers upon muridae from the same source appeared in 1940 and 1941. The mammals of the Lake Eyre Basin had been dealt with earlier (1931-39). Since 1945 enquiry and further field work have been extended to areas of the Northern Territory to the north and east of the main reserve. In the present series of papers the term "Central" is used for the whole tract covered without reference to political boundaries, since conditions as they effect the ecology of mammals are not sensibly different in the three sections.

The summaries of distribution of most species are given in broad outline only and are subject to future modification. The sparse and fluctuating occurrence of many of the surviving mammals, the vast areas involved and the confusion caused by European occupation, make a more detailed treatment impossible. All that is attempted here is to quote localities for all material examined, to add the results

of personal observation and of enquiry among natives and correspondents, and to combine this with existing records, many of them little known and scattered through the literature of exploration and surveys. The body of data assembled in this way, provides a considerable advance both in scope and accuracy on the information previously available, but anything approaching a satisfactory survey, has long since ceased to be possible. Systematic interrogation of aborigines, with authentic specimens to stimulate interest and facilitate comparison, has long been practised by the writer and has proved a most fruitful source of information. When subject to checking and cross checking among the older people of widely separated and independent groups, such testimony can be refined to a high degree of utility, and it is keenly to be regretted that the chaos into which aboriginal life has sunk, has brought this source almost to an end.

The data and material obtained on these private expeditions has formed the nucleus on which the following reports are based, but in addition, much other relevant material in the South Australian Museum has been consulted. In reviewing the morphology of Central Australian species, one of the chief aims has been to provide a reliable description of an authentic series, which might serve as a basis for comparison with other populations when such are available, and so shed light on the degrees of subspecific differentiation mentioned above. In some cases also where fossil or subfossil material has been available in sufficient amount, such a comparison has given useful information on the Post Pleistocene history of the species. In this work metrical data in the form of ranges and approximate means of dimensions and indices has been freely used in arriving at tentative conclusions, but conventional statistical analysis is deferred. It has been necessary to distinguish a few well marked forms by nomenclature, but in general I have been chary of adding new names for such differences as have been demonstrated and taxonomic treatment along trinomial lines has not been consistently followed. In the present state of the development of the subject, such a course, even if desired, is a hazardous one owing to the frequent inaccessibility of type specimens and the impossibility of forming just estimates of the normal range of variation in the species they represent.

In this connection it may be noted, that within the Central Australian field itself, conditions as they apply to ground living mammals are especially ill adapted to the operation of the *Formenkreise* type of mechanism, which underlies the theory of the development of the

geographic subspecies. Over vast areas of the country, the ecological gradient is exceedingly low and physical barriers to the free movement, even of small forms are absent. On the other hand, climatic factors in the form of sparse and irregular rainfall, exert cataclysmic effects by periodic depopulation of whole districts during drought and repopulation of the same by the breaking of drought. These population movements are almost entirely capricious in direction, and in mammals of high mobility and dispersal capacity result in a constant mingling of communities over areas so wide that regional differentiation of a permanent character is largely suppressed.

***Bettongia lesueuri* Quoy and Gaimard 1824**

Originally described from Dirk Hartog Island in Shark Bay on the Western Australian coast in lat. 26° South, this rat kangaroo has since been shown to have had one of the most extensive continental ranges of any of the Australian marsupials, reaching from about 14° South lat. in the north-west down to the extremity of the south-east coast in lat. $37^{\circ} 50'$ South, and from the west coast almost across to the eastern cordillera in New South Wales. The north-eastern sector embracing most of Queensland and part of New South Wales has yielded no published records of the species and thus forms an interesting hiatus in its distribution, but whether of fact or merely record, is somewhat doubtful (fig. 1).

The range has frequently been given as Western and South Australia and this has misled many writers, even in recent years, to overlook its former presence in Victoria and New South Wales. That it occurred in the Murray districts of these States in 1863 was plainly attested by Krefft in Lydekker (1894) and more doubtfully, in northern New South Wales in 1865 by Macgillivray (in Iredale 1937). Tate (1948) has also published evidence of its occurrence in Victoria.

The former habitat included a wide range of climates but wherever it occurred it seems to have followed a fossorial way of life on more or less open plains, and has shown itself, especially in arid districts, markedly intolerant of pastoral occupation, so that both its numbers and dispersion have been greatly reduced from what obtained primitively. Nevertheless, it still occupies large areas in the States of Western and South Australia and the Northern Territory.

Two races have been separated from the original insular form; *B. lesueuri grayi* Gould 1840 based on the Swan River in Western Australia and *B. lesueuri harveyi* Waterhouse 1842 from Eyre

Peninsula, South Australia. In addition, the insular form *B. lesueuri* Quoy and Gaimard 1824, has now been accorded a representation on the adjoining mainland by Chauert (1950). While these names have been widely used, the morphological basis on which they have rested is of the flimsiest, and as Harper (1945) has pointed out, the lines of demarcation or intergradation between the forms are quite unknown.

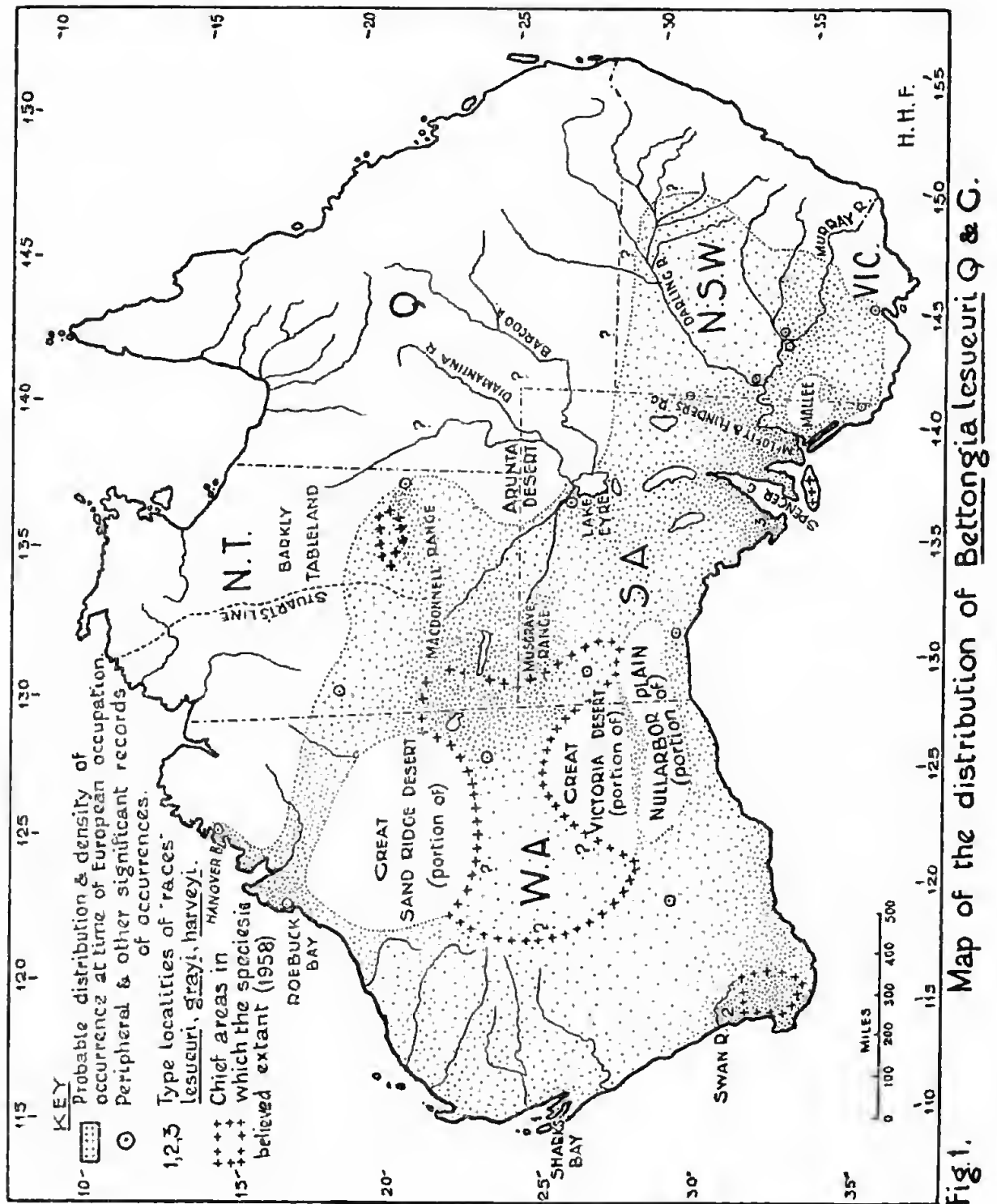
The material in hand comprises series from both Central Australia and the lower districts of South Australia, and these will be considered separately.

THE CENTRAL AUSTRALIAN REPRESENTATIVE

DISTRIBUTION AND HABITS: The former distribution in the Centre was wide (fig. 1), but its limits can now be but vaguely indicated in all those areas which have been under pastoral occupation for long. Probably its greatest stronghold was along the east-west axis of the Macdonnell Range system and in the south-west sector in and about what are now the great Aboriginal Reserves on the borders of the three States. As late as 1940 it was still numerous here, particularly so in the Musgrave-Everard Range area from which it extended with increasing sparseness into the north-west districts of South Australia, to about lat. 30° South. Forty years before this, at about the turn of the century, its colonies were continuous over the western half of the latter State, as far down as the Adelaide-Wakefield plain.

Of its northern extension, there is little satisfactory evidence, but I place its limit provisionally at about 20° South lat. To the west of Stuart's line in this latitude it may extend somewhat further north, but to the east of it, the Barkly Tableland was apparently never occupied, and interrogation of Wombaia survivors there has given only negative results.

The eastern limits lie near the Queensland border. It is well known to the eastern Arunta and the Ilyowra, and remained within their territory between the Plenty and Sandover Rivers until the late 1920's. The Wonkanooroo have a name for it in the south-eastern extremity of the Arunta desert but it was not reported by either Colson in 1938 or Madigan in 1939 in their traverses of the central portion of this region. South of the Arunta Desert, Andrews (1876) collected it in 1874 in the Lake Eyre district probably on the Macumba at the north end, and Sanger (1882) recorded it from the lower Cooper on the east side. Sanger's account of it, however, is more



suggestive of *Caloprymnus* than *B. lesueuri* and in 1931 I was unable to get any positive evidence of the latter in this part of the Lake Eyre Basin. Longman (1930) does not record it as a Queensland species.

To the west, the records are few and derived chiefly from journals of exploration in the Sandridge, Gibson, and the Victoria Deserts and their value is uncertain owing to frequent confusion in the accounts with *Lagorchestes* spp. and *Thalacomys*, and the absence of material in support. However, I accept Giles' citation (1889) at approximately 24° 42' South and 127° 44' East in Gibson Desert in 1874 as the mode of occurrence is characteristic and I have taken it personally north of Desolation Glen in the Rawlinson Range, only 50 miles south-east of his locality. Carnegie's (1898) record from Wilson Cliffs in the Sandridge Desert at lat. 22° 1' South and 126° 57' East may perhaps relate to *Thalacomys*. The Canning Stock Route Expedition of 1931, which crossed about 100 miles west of Wilson Cliffs, recorded neither the animal nor its warrens, nor is there any recognizable account of the animal in J. Forrest's journal of the 1874 traverse along the 26° parallel, though in the latter case as in most early exploration, such negative evidence is not likely to be significant. The question of the isolation of these Central and South Australian populations of *B. lesueuri* from those of Western Australia, which has an obvious bearing on the validity of the three races named is thus left undecided by the published records. The case for continuity of distribution in the recent past, based on the continuity of available habitats is, however, a very strong one; even if the central portions of the three western deserts are regarded as impassable barriers, there remain three avenues of feasible intercommunication along three routes, *viz.* the coast lands of the Bight, the 26° parallel, and the north and eastern margin of the Sandridge Desert. In connection with the latter it may be noted that the large "rabbit" warrens recorded by M. Terry in 1929 in the Tanami district in approximately 28° South and 129° 51' East, would almost certainly be warrens of *B. lesueuri* doubtfully parasitized by rabbits.

Its present status (1958) is everywhere a rapidly dwindling one. It survives in very small numbers in the territory of the northern moiety of the Ilyowra and of the Worgaia to the east and north of the Elkedra (Ilketera) River, which has only recently been brought under pastoral occupation; possibly also, as an extremely attenuated remnant at one or two points in the drainage of the Sandover and Plenty Rivers, and in the Reserves of the south-western sector. In the latter its persistence will depend in large part on the extent to

which the fox is able to increase its range to the north. The southern portions of the Reserve have been heavily infiltrated by this pest in recent years and it is doubtful if it exists today in the Musgrave Range area, where it was in large numbers only twenty years ago.

The species formerly occupied a prominent place in aboriginal life and lore, in practical venery and in legend. Its identity is easily traceable in their accounts, by its habit, unique in the Macropodidae, of excavating large warrens for community dwelling and by its truculence. To the Pitjanjarra of the Reserves it is known as metika or tchungoo, and the second of these terms has a very wide usage, ranging in the north beyond the Rawlinson Range into Pintubi territory, while in the south recognizable variants of it can be traced as far as Ooldea. The western Arunta call it tnunka, but their eastern moiety have largely adopted the Ilyowra word, alutta, which in recent times they have carried into the Pituri creek and Toko range area on the Queensland border in lat. 22° 30' South approx. The original Wonkamunna of this district are now reduced to a very few individuals who no longer occupy their home territory, and in a recent visit to it I was unable to learn their name for the animal from their supplanters, or to fix definitely whether the species ever occurred there. However, it certainly extended to a point about half way between the Tarlton and Toko ranges, and within 50 miles of the border. These two names also have considerable extension to the north and are used or understood, far beyond the boundaries of the Arunta and Ilyowra as drawn by Tindale (1940). The Wonkanooroo and Dieri call it kanunka, which suggests a recent derivation from the Arunta word.

In 1931-35, before the fox had become a serious factor, I found it one of the most plentiful mammals of the Reserves. However, its numbers fluctuate greatly and its occurrence is local and discontinuous and not uniform. Warrens housing a big population during one season may be found quite deserted the next, though conditions have not greatly changed in the meantime. It has often been described as an animal of the "sandhills" but this is only true in the vernacular sense in which all areas away from rocky ranges, are so described. With the exception of rocky hills and ranges and dense thickets, it colonizes most types of country; grassy and herbaceous loam flats within the major ranges, open mulga and ironwood parks skirting the ranges, and penetrates deep into the true sandridge areas as well. Here as elsewhere, however, its warrens are usually made in the firm loam at slight elevations on undulating swales and not in the sandridges

proper. On the northern margin of the Amadeus Basin the burrowing is often done into slight outcrops of friable limestone and gypseous rock and in 1950 I noted a similar occurrence over a small area between the western Macdonnells and Stuart Bluff Range, though the animal has long been extinct there. This is the type of warren noted by Giles (*supra*) and is affected also apparently by the coastal colonies at Roebuck and Shark Bay.

In general, Central Australian warrens are much less complicated than those described in Western Australia by Gilbert in Gould (1855) and Dahl (1897). One excavated on a loam flat at Yaringa, south-west of the George Gill Range, went to a total depth of no more than four feet, at which level lay the main gallery from which two *tehungoos* were taken. Above this were many short off-shoots which were occupied by rabbits only and this arrangement is a frequent one but whether it is universal here as Wood Jones (1923-1925) avers it is further south, is doubtful. The burrowing habit is more fundamental in *tehungoos* than in rabbits, a large proportion of which in these latitudes lead a surface existence or make use of shallow excavations only for shelter or breeding. When the rabbit invaded the centre, abandoned or incompletely utilized *tehungoo* warrens were plentiful as they are now, and it seems more likely that the rabbit parasitized the *tehungoo* than *vice versa*, as has been suggested, and this is also the native version. No doubt the rabbit has introduced an adverse factor into the ecology of *B. lesueuri* as with other small native herbivores, but in the 60 years they have been together in the south-western areas of Central Australia, it has not proved a fatal one, and but for the increase of the fox it might have continued to enjoy a somewhat reduced tenure, indefinitely. In areas of pastoral occupation still other factors are superimposed by the presence of stock, with which it cannot cope.

It is extremely shy and cautious, strictly nocturnal and in summer at least, leaves the warrens only long after dark and is a most difficult animal to observe under natural conditions, even when it is plentiful. In the accounts of the Horn Expedition and of some of the explorers it is confused with *Lagorchestes hirsutus* which is often seen in daylight in spinifex tracts. The *tehungoo*, however, is not normally found in such country but burrows in areas where the small plant cover tends to be rather varied with *salsolae* and succulents such as *Calandrinia* and *Portulaca* and when large warrens are occupied, its pads—*tehungoo* roads in local parlance—are often conspicuous,

radiating out to its feeding grounds. The track nearly always shows a distinct imprint of the tail between those of the feet, and these are wider apart than in *Lagorchestes*.

In addition to the green parts of a large number of plants, it excavates and eats quantities of bulbs and tubers, of which the roots of the very widely spread procumbent species, *Boerhaavia diffusa*, are the most important (Pitjanjarra, karrpilba; Ilyowra, ayepa). The bulbs of the yelka or nut grass, *Cyperus bulbosus*, and of a lily called by the Ilyowra ilgelgunya (*Crinum* sp.) are also sought out, as well as an unidentified yamlike product known as poonba in the Musgrave Range area. In the south-west sector, where the quondong (*Eucarya acuminata*) is plentiful, its fruits (waianoo, mangada) are an important item of diet and are taken down into its burrows in quantity. Not only is the fleshy rind eaten but, like the local *Notomys*, it makes use of the oily kernel of the nut as well, which necessitates gnawing away a large part of the flinty hard casing; a task for which the stout rodentlike first incisors are well adapted (Pl. xxvii, fig. H; Pl. xxviii, fig. A).

Under present day conditions it is not easy to get undamaged specimens. It is wary of traps especially on warrens and when caught in the ordinary types of small steel trap is difficult to hold owing to its fragile limbs. A good many are taken accidentally by doggers in the much larger dog trap which often takes the animal by the middle and prevents struggling. Practically the only way of getting it undamaged is by digging it out which is extremely laborious. It is powerful for its size and when taken from a burrow struggles violently and scratches and bites severely, making the while a harsh aspirant sound with occasional grunts. The latter I presume is the call which it has often been stated to make at night when abroad, though I have never heard it thus in the Centre.

On moonlight nights the blacks occasionally take them when feeding away from the warrens, either by the spear or with dogs, and if pressed for food, the women will sometimes dig out the smaller burrows, though nowadays the labour involved is out of all proportion to the probable results. In the heyday of the species on the Sandover River, where for a time it was in very large numbers, the Ilyowra practised some ingenious methods of shortening this labour. Having selected a large and well populated warren, a party of men working in the middle hours of the night, when the animals were away feeding, securely blocked up the entrances to all the deep burrows, but left

open a number of shallow experimental drives which were always present on the outskirts of the larger warrens. The aluttas, returning before dawn, were thrown into confusion by this denial of their accustomed refuge, and after frantic but unavailing efforts to clear the entrances, were forced by the rising sun to take shelter in the shallow drives. Here they were promptly stupefied with smoke to prevent them digging deeper (which they otherwise do very expeditiously) and were then dug out in numbers with little trouble. They were much relished as meat. Thirty-five years ago, towards the end of their major tenure of the Ilyowra country, their way of life became considerably disorganized and a portion of the remnant forsook the warrens and lived in holes in creek banks.

From most nonhuman predators it was well protected by its strictly nocturnal feeding and deep burrowing habit, but the largest of the local lizards (*Varanus giganteus*), a voracious creature, attacked it in the warrens, and took considerable toll.

The specimens personally examined have been free from the larger ectoparasites. The animal has no characteristic smell. Reproduction appears to extend over the greater part of the year and pouch embryos and young, up to 170 mm. long, have been obtained both in mid-summer and mid-winter.

EXTERNAL CHARACTERS: The material examined represents 32 individuals, obtained from the following localities, all in the south-western sector: (a) Chundrinna, N.W. of the Everard Range at lat. $26^{\circ} 51' S.$ and $132^{\circ} 13' E.$; (b) several other points between Chundrinna and the southern front of the Musgrave Range; (c) Allarinna, on the northern front of the Musgrave Range; (d) near Murrachurra Spring, 20 miles east of Mount Conner in lat. $25^{\circ} 26' S.$ and $132^{\circ} 13' E.$; (e) Yaringa, 12 miles S.W. of King's Creek in the George Gill Range; (f) north of Desolation Glen in the Rawlinson Range at about $24^{\circ} 53' S.$ and $128^{\circ} 16' E.$ That portion of the series which is sexed comprises 12 σ , 13 φ .

Wood Jones (1923-1925) has given an extended account of the external characters of a series from the Lake Phillipson area and as the present material is in substantial agreement with his, a full description is dispensed with and the following supplementary notes substituted.

His illustration of the *head* gives a much better impression of the appearance of the living animal than earlier figures; the deep abruptly truncated muzzle is especially characteristic and in this point it differs

from its congeners while somewhat resembling *Caloprymnus*. In life the rhinarium is bluish pink and its upper margin is evenly convex and not spurred upwards in the centre. The facial vibrissae are well developed though slender; the genals and supraorbitals are unusually large and exceed the mysticals. The ear backs are evenly convex and without indentation as in *Caloprymnus*.

In the *manus* the palm is yellowish white and coarsely granular; the palmar pad being less developed than in *Caloprymnus*. The digital formula based on the distal extension of the digits is $3>2>4>5>1$ as given by Wood Jones, but the disproportion in general development of the three central digits is slight and the formula for size is $3>4>or = 2>5>1$; the claws are white and translucent. In the *pes*, the plantar surface where exposed is yellowish white, and coarsely granular over its whole extent whether covered or exposed; at about the mid point of the metatarsus the granules are hexagonal and average 15 per cm. but elsewhere they vary much in shape and are often irregular. The encroaching of the hairs from the dorsum of the foot over the plantar surface is a constant feature in all young and young-adult animals and the condition is usually much as figured by Wood Jones (*op. cit.*, fig. 155). The hairs at this stage are not felted down into a mat but are arranged in two overlapping layers taking origin in opposite margins of the dorsal surface and remaining quite separate; the development of hair is profuse and the insulation of the less calloused portions of the sole and digits, very effective. In old animals, however, the hairs are thinned out by abrasion and the entire plantar surface of *pes* and digits is not infrequently quite naked. The apical segment of the fourth digit is much less expanded than in *Caloprymnus* or *Aepyprymnus*, and the elements of the main interdigital pad are sometimes incompletely fused as in *Potorous*, a shallow sulcus dividing it into two longitudinal moieties. The nails of the digits are yellowish white and translucent.

The *tail* is nearly circular in section and tapers slowly to its apex; calloused areas are not developed upon it. The pouch opening is posterior to the mid point of the ventral length and the space intervening between its lower margin and the cloaca is often nearly nude, and sharply defined by laterally diverging hair tracts. The *cloaca* has no enlarged bristles, but a short fleshy process is developed on its posterior margin, similar to but smaller, than that which I have recorded for *Caloprymnus* (1932). No sternal gland has been observed.

Secondary sexual differences are slight; the male is not superior to the female in linear dimensions, but is more massive, with a thicker blunter head, and deeper muzzle, and heavier feet.

PELAGE: The general colouration viewed from a distance of a few feet varies in different individuals from grizzled buff grey to grey brown with lighter ventrum and the head and appendages distinctly contrasted in warmer buff and tan. At its best the pelage is dense and soft; mid dorsally the main pile reaches 22 mm. with guard hairs to 30 mm., lengthening on sides to 25 mm. and 33 mm. respectively. The basal half of the main pile is about Ridgway's slate grey, the succeeding third forms a sharply contrasted band varying in different individuals from light buff, to tulle buff, and the extreme tip clove brown. The guard hairs are slate grey in the shaft, with a narrow brown band separating it from the flattened blade which varies from ivory yellow to near white and the extreme tip shades off from sepia to black; a small proportion of guard hairs are dark throughout. The composition of the pelage is thus similar to that of *Caloprymnus* but the overlay of ivory and white is much less profuse and has less effect on the general ground colour, which ranges from deep olive buff to light brownish olive.

The sides are similar to the dorsum, but paler and less grizzled and are sometimes separated from the ventrum by a lateral line of rich buff. The ventral fur averages 17 mm. with a sparse overlay reaching 30 mm.; it is mostly bicolor, with a basal zone of slate grey almost obscured by the terminal colour which is creamy white variably washed and dappled with warm buff. The scrotum, small areas on the throat, and mid belly are creamy white to the base. The head is more warmly coloured than the body, the ground colour varying from tawny olive to cinnamon buff; on the muzzle it is closely grizzled with brown and buff but the crown and genal surfaces are more uniform. The inner surfaces of the ear are nearly nude except distally where they are sparsely covered with short adpressed cinnamon buff hairs. Externally the ear backs are well covered with loose fluffy fur, slate at base, rich tawny olive terminally and conspicuously bordered at the anterior margin with clove brown.

The forelimb is externally long haired, buff dulled by the basal slate colour; internally somewhat lighter; the manus densely clothed with adpressed hairs of clear cinnamon buff lengthening over the base of digits but not obscuring the claws. The hind limb is externally like the sides or rather darker and sometimes has a poorly developed

lighter hip stripe. The pes also is cinnamon buff or slightly richer and has a tendency to darken on the outer metatarsal surface and the fifth digit. Its hairing is close, short and dense dorsally, but is greatly lengthened on the sides so as to overlap and obscure large areas on the plantar aspect of the digits. In most examples the digits of both manus and pes are stained a bright orange tan by clay dust; this can be completely removed by mild detergents leaving the colour the prevailing buff. The immediate tail base is clad with dorsal body fur which gives place suddenly to short coarse hairs, which are closely adpressed except on the terminal third of its dorsum, where a progressive lengthening begins. Laterally and ventrally the colour is uniform cinnamon buff, but dorsally this is darkened by a pencilling of brown, increasing distally until it completely replaces the buff ground colour of the subterminal fifth or more by rich prout's brown to clove brown. The apex of the tail for distances averaging 35 mm., is pure white on all surfaces when unstained and dorsally its hairs are lengthened to 20 mm. and frequently form, especially in subadults, a distinct erect crest. The tail is everywhere densely clad and its scutination completely obscured.

Variation of the pelage in density, texture, degree of grizzling and ground colour is considerable, but in the present series cannot be satisfactorily linked with local, seasonal, or sex factors. The shabbiest coats with the darkest ground colour are found in winter months, when rump abrasion is often marked; but dense, even, richly coloured coats and their opposites occur at all times of the year and there is little evidence of a seasonal moult affecting members of a colony, simultaneously. The coat in subadults as late as the P³M² stage, is often looser, with a greater exposure of ground colour than in adults.

Wood Jones (*op. cit.*) comments on the fugitive nature of the "yellow" colouration in this species. I find that field skins in my own collection, personally made in 1932 and 1933, and which have had no contact with liquid preservatives and have been stored in the dark, still show the original colouration as noted on the freshly killed animals at the time. Others in the South Australian Museum of the same provenance which were treated there by immersion in alum and salt pickle, show a more or less marked change of olivaceous ground colour to warmer browns, which are not normal to the living animal, and there is a variable degree of bleaching of the cinnamon buff of the appendages.

Under the name "*Bettongia lesueur graii*" Gould, Boardman (1949) has described the hair tracts in an advanced pouch young from

Bernier Island, which however, would more conventionally be regarded as representing the typical race *B. lesueuri lesueuri* of Quoy and Gaimard. In the present series, examples suitable for checking the primary tracts are lacking, but in adults, except for small suprarhinal and preorbital divergences, the external pelage over the entire dorsal surface is directed uniformly caudad, and on the limbs distad, the postaxial trends of the latter being largely obscured. In undisturbed material the ventral inclination of the lateral fur is slight and there is no median opposition ridge on the ventrum, as is frequent in *Caloprymnus*. A reversed gular tract, directed forward and outward is constant, and radial tracts diverging from the pouch margins and precloacal areas of females, and the scrotal area of males, can usually be made out. In general, interruptions to the primitive caudad flow in the adult pelage, are much less in evidence on both dorsum and ventrum, than in most Macropodinae.

DIMENSIONS: The range and mean values in mms. of conventional measurements for a bisexual series of eight fully adult individuals at the P⁴M⁴ stage, is given in tabular form on p. 267. Even when age changes are thus drastically restricted, the variation in all items is high, reaching 26% in the head and body length. Sexual differentiation is inappreciable, the adult female being as large as the male. Maximum dimensions for ear and pes are often attained as early as the P³M² stage. The tail is always shorter than the head and body in adults, but may be subequal in younger animals.

The following figures give the detailed measurements of a subadult ♀ (P³M³) from Yaringa Creek, at the western end of the George Gill Range, in Central Australia: head and body, 285; tail, 285; chest, 150; length of manus, 24; nail of third digit, 9; pes, 101; 4th toe, 42; nail of 4th toe, 17; ear, 36 x 22; rhinarium to eye, 31; eye to ear, 25; eye (intercanthal), 11; weight in grammes, 910.

Weights of adults are not available, but would probably reach 2,000 grammes.

CRANIAL CHARACTERS (Pl. xxvii, fig. A-II): Both skull and dentition of *B. lesueuri* present notable features which have been imperfectly described and some of these separate it decidedly from its congeners, by making an approach (especially in dentition), to the more advanced condition of *Aepyprymnus* and *Caloprymnus*.

Since existing descriptions give little information on the variation which occurs, and are based for the most part on mixed series from several localities, the whole question of subspecific variation on these

important heads, remains quite vague. In the present work, 72 skulls, (the majority of them not sexed), from South, Central and Western Australia have been used in examining the cranial and dental characters of the species as a whole; fifteen of these, taken from individuals of known external characters, represent the Central Australian population, and these alone form the basis of the following description. Differences shown by material from other localities, are dealt with in the sequel, using this homogeneous series, as a standard of comparison.

Intrinsic variation within the series, is high, both in non-metrical morphology and dimensions; in a series of 23 cranial and mandibular measurements the percentage variation in adults ranges from 7.5-40%, with a mean of 15%. Many of the most salient features of the skull observed singly, such as the development of the rostrum, size and shape of nasals, width of zygomatic arch and interorbital region (which are very apt to give premature impressions of subspecific difference) are subject to marked individual variation.

The skull is densely ossified, with strong muscle ridging, and with the mandible, attains a maximum weight of 19 grammes; it is the shortest and widest in the genus and in this respect is equalled by *Caloprymnus* alone amongst the Potoroinae, the length \div breadth ratio falling as low as 1.5. The maximum zygomatic width is usually posterior, but wide variations occur in the overall zygomatic outline, which is sometimes similar to *Trichosurus vulpecula*.

The muzzle region is short deep and less conical than usual, and the mean facial index of 181 is one of the lowest for the subfamily. The nasal bones reach or slightly exceed the level of the anterior margins of the orbits; their length \div breadth ratio is variable as is also their overall shape and the combined posterior margin may be almost transverse, sharply angulate or invaginate in the mid line; there is always a distinct and sometimes a sudden, constriction of their width just anterior to the maxillo-premaxillary suture. The interorbital area of the frontals is of medium width averaging 25% of the basal length; but is parallel sided until late in life when the free margins converge slightly to form a moderate intertemporal constriction. The supraorbital ridges are sharp and overhanging and occasionally develop rudimentary postorbital processes. The variability of the coronal portion of the frontoparietal suture mentioned by Wood Jones (*op. cit.*, p. 209) is well illustrated but the transverse condition is the commoner. The development of the temporal ridges

reaches a maximum for the subfamily in *B. lesueuri*, but their confluence on the parietals is very posterior and a sagittal crest as in *Potorous tridactylus* is not formed. At a lower level on the vault, the squamosal suture is often strongly ridged. A crescentic interparietal is long persistent and overlaps in part the supraoccipital on the lambdoid crest, which is but moderately developed.

The occipital plane is nearly vertical and deeply indented and its arch is low and broad; the paraoccipital process is well developed and distinct posteriorly though its anterior surface is closely applied to the bulla and it has little free projection.

On the lateral aspect, the premaxilla is reduced, though less so than in *Aepyprymnus*, and still makes an important contribution to the wall of the nasal cavity; its suture with the nasal is about equal in length to that of the maxilla. The facial plate of the lacrymal has from $\frac{1}{2}$ to $\frac{3}{4}$ the area of the orbital plate; the lower foramen in adults is usually larger than the upper, but they may be subequal and are occasionally confluent. The zygomata, especially the malar contribution, are relatively much the most powerful in the Potoroinae, and the infrazygomatic process of the maxilla, though it falls far below the standard of *Caloprymnus* and the Macropodinae, is distinctly indicated. The area of the temporal pterion is rugose and deeply impressed and the series inspected affords no exception to, nor important variant of, the frontal-squamosal contact, which, following Owen's original observation (1866) now proves to be constant for the subfamily (Finlayson 1932, 162, and Pearson 1950, 213-221). The diastema, with that of *Aepyprymnus*, is relatively the shortest in the subfamily, and the posterior palate is one of the narrowest; its posterior vacuities are also long and narrow and occupy almost the whole of the intermolar space, the medium septum and posterior bar being reduced to fragile remnants often lost by damage; their anterior extension varies from the middle of M^1 to its anterior margin, and a pair of small foramina sometimes lie beyond this. The anterior palatal foramina are exceedingly variable, the length fluctuating over a 40% range.

The enormous expansion of the alisphenoid bulla is perhaps the most conspicuous specialization of the skull, though it comes as a culmination of a well marked tendency in the Potoroinae, and is less remarkable in the Macropodidae as a whole since the discovery of *Lagorchestes asomatus* which approaches it in this character. Nevertheless the bulla in *B. lesueuri* is probably the largest in relative volume in the Marsupialia and has comparatively few rivals in the

whole of the Mammals. In the prepared skull, owing to the incomplete condition of the upper rim of the tympanic annulus, the bulla communicates freely with accessory cavities in the posterior root of the zygoma and adjoining parts of the squamosal; the condition in varying degree is general throughout the Potoroinae but is especially developed in *B. lesueuri*. While the habits of *L. asomatus* are unknown, *B. lesueuri* remains unique in the Macropodidae as a fossorial adept and in seeking some functional correlation of the enlarged bulla, this fact inevitably comes to mind, and receives some support from the fossorial and strongly bullate *Thalacomys* of the same region. However, the conflicting evidence of the fossorial and non bullate wombats amongst marsupials, and bullate and non bullate rodents of burrowing habits must leave the matter an open one.

Tate (1948, p. 241) has noted a condition in the mastoid squamosal region in which the Phalangeridae and Macropodidae differ. I find that the same area has differential value both at sub-family and species rank, within the latter. In the Macropodinae with few and partial exceptions, the mastoid margin of the squamosal and the root of the zygomatic process are separated by a deep fissure above the tympanic annulus. In all genera of Potoroinae persistent attempts are made to bridge this gap, by the outgrowth of a delicate flange-like process from the mastoid margin of the squamosal, which narrows the fissure to a channel. In *B. lesueuri* alone, this channel is in old age sometimes converted into a closed canal by a separately ossified plate joining the flange to the zygoma root (Pl. xxvii, fig. F).

The mandible is distinguished by the stoutness and convexity of the lower border of the horizontal body below the molar rows, the width and relative erectness of the ascending process, and the extension of the angular process into a slender style conforming to the contours of the bulla. The confluence of the pterygoid and masseteric fossae, is wide as noted by Tate, but very variable, and the masseteric canal is very large. Abbie has suggested that the latter is a functional correlation in the Potoroinae to the presence of a large premolar, but the relative development of the canal seems to bear no simple relation to the size of the premolar or the length of the jaw in the different species, as one would expect if this were so. *Potorous tridactylus* with a long slender jaw, and comparatively small P⁴ has the canal as strongly developed as *B. lesueuri*, where these proportions are reversed. Moreover the long slender jaw of *Dorcopsis luctuosa* which supports an enormous premolar (both absolutely and relatively larger

than anything shown by the Potoroinae), makes no departure from the meagre development of the canal general in the Macropodinae.

The evidence of sexual differentiation is unsatisfactory, being supported on the female side by two adult skulls only, but so far as it may be accepted indicates that cranial differences are slight. The female skull tends to be slightly smaller, with shorter nasals, wider interorbital space, longer anterior palatal foramina and a higher facial index. Muscular impressions tend to be less in aged females than in aged males. Age changes are not marked and their recognition is complicated by irregularities in dental succession and individual variation. This leads to a wide overlap in dimensions and structural detail between different dental groups; thus skulls as early dentally as P^3M^2 may be as large in overall size as aged skulls of the same sex at P^4M^4 .

DIMENSIONS: As the sexual factor cannot be accurately assessed in any of the three recent populations and scarcely at all in the sub-fossil one, but is known to be slight, comparisons have been made for the most part with bisexual series. The following figures give the range and approx. mean of skull measurements of (1) a bisexual series of 8 at P^4M^4 and (2) 3 females at P^3M^3 : greatest length, 64.3-73.3 (69.2), 62.3-65.3 (63.4); basal length, 54.2-60.2 (57.2), 52.3-52.6 (52.5); zygomatic breadth, 40.5-45.6 (43.0), 38.7-40.6 (39.9); nasals length, 22.8-28.6 (26.3), 22.5-24.9 (23.6); do. greatest breadth, 11.1-13.4 (12.4), 10.7-12.1 (11.6); do. least breadth, 4.9-6.8 (5.9), 5.2-5.5 (5.3); depth rostrum, 12.0-13.6 (13.0), 11.3-12.9 (11.8); interorbital constriction, 13.2-16.3 (14.5), 14.0-15.4 (14.5); palate length, 34.8-38.0 (36.4), 31.4-34.9 (32.8); do. breadth inside M^2 , 9.8-12.2 (11.3), 9.5-11.1 (10.4); ant. palatal foramina, 2.2-3.8 (2.8), 2.0-2.8 (2.5); diastema, 7.3-9.0 (7.6), 6.0-8.4 (6.8); bulla length, 15.1-17.0 (15.9), 14.3-16.6 (15.0); bulla breadth, 11.0-13.3 (12.2), 11.2-12.1 (11.6); facial index, 171-191 (181), 166-197 (179); mandible, maximum breadth, 40.2-44.0 (41.7), 36.5-38.8 (37.9), maximum depth below M_2 , 8.1-10.0 (8.8), 6.6-8.6 (7.6); breadth ascending process, 13.7-16.3 (14.8), 12.5-13.5 (13.0).

DENTITION (Pl. xxviii, fig. A-M): Variation in linear dimensions of teeth not rapidly altered by wear, such as the premolars and molars, ranges from 5-34% with a mean of 15%.

The incisors, as a group are relatively large and functionally important teeth, by the standards of the genus, and they sustain heavy wear. As a result the 1st and 2nd are subject during life to marked changes of size and shape. I^1 when unworn has a broad alveolar base

tapering to a pointed apex; growth is persistent however over a large part of the life span and as the tooth is extruded the apex is worn back to a chisel edge which steadily widens until it yields the maximum diameter of the tooth. Its size dominance over I^2 and I^3 is greater than in *B. cuniculus* or *B. penicillata* and tends to increase with age, and from $\frac{1}{2}$ to $\frac{3}{4}$ of its height projects beyond their working level. The dorsoventral height ranges in the present series from 4.9-7.9 mm. and its antero-posterior diameter from 2.2-3.0 mm. Both Thomas and Waterhouse claimed that a broader and flatter I^1 was diagnostic of *B. lesueuri*, but the material in hand does not support this. There is however a noticeable rotation of the tooth with advancing age, so that its labial wall becomes more and more anterior in aspect and less lateral.

I^2 is relatively constant, reaching a maximum antero-posterior length of 3.0 mm. in young skulls and a transverse breadth of 2.1. I^3 when unworn is comparatively narrow and upright with a vertical height of 3.1-3.6 mm. and antero-posterior length of 2.0-2.6; with age, it is thrust forward more and more and obliquity of wear may increase the latter value to 3.3 mm. The transverse broadening of I^2 and the inturning of the cutting edge of I^3 are both more marked than in other bettongs and foreshadow the extreme condition of *Aepyprymnus*.

The lower incisor is comparatively stout for the genus but shows all the differential characters separating the Potoroinae from the Macropodinae in this feature; i.e., its great absolute length and relative narrowness, maximum width at alveolus with evenly tapering outline to the apex, absence of median expansion of the blade, and of abrupt incurving of the upper margins. In adults of moderate wear, the anteroposterior length from alveolus is 10.6-11.4, and this is maintained or even increased in very old animals, where the shaft of the tooth may be completely denuded of enamel. The maximum transverse breadth of enamel ranges from 2.7-3.1 and shows considerable resistance to age changes until late in adult life, though its site moves steadily distad. On the other hand the maximum breadth of the tooth as a whole, including dentine, increases markedly with age and is always proximal; in eight adults it varies from 3.2-4.3.

The canine is well developed but variable in size, shape and inclination. In the young fully enamelled condition it is flattened and incisiform, with the labial face nearly as large as that of I^3 , and with a vertical height of 3 mm. ca. and anteroposterior breadth of 2.2 mm.

As wear advances the apex becomes more pointed, the recurvature is accentuated and both height of the tooth and width of root exposure in alveolus may increase to 3.7 mm. The premaxillary suture bisects its alveolus and the tooth is always much nearer to the 3rd incisor than to either of the premolars. Although clearly a functionally important tooth its apex never descends much below the middle of I³.

In the permanent premolars, *B. lesueuri* illustrates in an extreme degree the general trend of the Potoroinae towards enlargement, suppression of cusps and vertical corrugation. P⁴ is a narrow and usually almost parallel and straight sided blade and in relation to skull size is by far the largest tooth in the subfamily. Wear is heavy, but is chiefly seen in removal of the surface grooves, and reduction of the height of the blade; the latter may fall from 3.8 mm. to 1.7 mm. while length and breadth are almost unchanged. In taloned forms of the tooth, the maximum breadth is always posterior, otherwise at about the anterior third. Both the crest of the blade and the enamelled wall of the crown are of nearly even height throughout its length, the main posterior cusp alone being sometimes slightly raised; in 10-grooved examples the anterior cusp is scarcely differentiated. The number of grooves on the external wall varies from 8 to 10; 9 being present in 50% of examples and 8 and 10 occurring with equal frequency in the remainder. The grooves may form an even series of shallow crescents with the convexity anterior or they may have a more or less radial arrangement converging postero ventrally to a common centre below the posterior angle of the crest. The normal inclination of the long axis of the tooth is evenly anterointernal towards the midline of the palate; rarely it may be parallel but never extraverted as in *penicillata*.

A point of some general significance with P⁴ is the variability of the postero-internal talon and its cusp and the internal ledge—structures which in the Macropodinae are regarded as of great specific integrity. In *B. lesueuri* of this series, both may be completely absent or strongly developed in premolars of the same degree of wear (Pl. xxviii, fig. F and G), and the talon is sometimes accompanied by a posterior fossette. Anteroposterior length of unworn or slightly worn examples ranges from 7.6-8.7 mm, with a mean of (8.2), transverse breadth 2.5-3.3 (3.0) and vertical height of enamel 3.2-3.8 (3.5).

The lower secatur P₄, is a simplified and somewhat reduced version of the upper, with length and breadth about 15% less but with the height of the blade retained. The maximum breadth may be

either posterior or anterior or at both, but never median. External grooves vary from 8 to 10 and generally conform to those of its opponent; where the number differs, the lower tooth generally has the fewer. The talon and internal ledge are almost completely suppressed. Antero-posterior length 6.5-7.3 (7.0); transverse breadth 2.5-2.8 (2.7); vertical height of enamel crown 3.2-3.8 (3.5).

The 3rd upper premolar P^3 is a much shorter and broader tooth than the secator; its maximum width is always median and its outline oval in superior view. The talon is absent, but the internal ledge variably developed, and either 5 or 6 grooves are present on the external wall with equal frequency; the grooves are commonly almost intact when the tooth is shed. The 3rd lower premolar P_3 is similar to the upper and is reduced in about the same proportion as the lower secator. Its outline is slightly reniform, the lingual wall being concave with the crest of the blade conforming to this curvature; grooves 5 or 6. Seven examples of upper and lower 3rd premolars, derived from skulls showing a rather wide range of development, have the following dimensions, respectively:—antero posterior length, 4.7-5.4 (5.0), 4.0-4.9 (4.5); transverse breadth, 2.7-3.1 (2.9), 2.3-2.8 (2.5); height of enamel crown, 2.7-3.2 (2.9); 2.9-3.3 (3.1).

The upper deciduous premolar MP^4 , is of the usual quadrate molariform type and is frequently as large as the third true molar. Its chief interest lies in the sectorial modification of the antero external cusp, augmenting the blade of the contiguous P^3 . I first drew attention to this feature in *Aepyprymnus* (1931) where it is very strongly developed and Tate (1948, 249) has since discussed it in other genera. In *B. lesueuri*, it is well, though variably developed in both upper and lower series. The mandibular tooth MP_4 is trigonid the anterior lobe being almost monopolized by the secant antero-internal cusp; it remains however four rooted. In size MP_4 is much inferior to M_3 . The following are the dimensions of MP^4 and MP_4 respectively in the 7 subadult skulls; antero-posterior length, 3.3-3.8 (3.5), 3.3-3.5 (3.3); breadth anterior lobe, 2.8-3.2 (3.0), 1.8-2.5 (2.2); breadth posterior lobe, 3.3-3.7 (3.5), 2.7-3.0 (2.9).

The upper molar rows, in distinction from *B. cuniculus* and *B. penicillata* are decidedly arched, with the greater convergence posterior. The effect is accentuated by the rapid diminution, in overall size and especially of transverse breadth, of the 2 posterior molars, which is a marked though not exclusive characteristic in *B. lesueuri*. Tate (1948, 269) has recently redirected attention to the

difference between the Potoroinae and Macropodinae in molar formulae and has published some dimensions of the molars of 3 examples of *B. lesueuri*. As noted earlier by Wood Jones, however, there is much individual variation in this regard, and in the present series the range in dimensions is wider than given by Tate. I find also, that in expressing the general size relations of the molars as functional units, an approximation to the *sectional crown area* is a more convenient and more adequate criterion than linear dimensions alone, and the formulae which follow are based on the values of $1 \left(\frac{ab+pb}{2} \right)$, where 1 is the anteroposterior length, and ab and pb are the transverse breadths of the anterior and posterior lobes, respectively.

In the upper molars the sequence $M^2 > M^1 > M^3 > M^4$ occurs in 5 of the 7 completed dentitions measured, the other 2 showing the alternatives $M^1 > M^2 > M^3 > M^4$ and $M^1 = M^2 > M^3 > M^4$ the position of M^3 and M^4 being constant throughout. In the remaining 8 skulls, $M^2 > M^1$ holds in all, and $M^1 > M^3$ in the 3 examples in which the latter tooth has erupted. Clearly therefore there is a high degree of probability, that on completion of the molar series in the subadult examples, 13 of the 15 examples (87% ca.) would show the dominant 2.1.3.4. sequence. The frequencies quoted later in comparing populations have been deduced in this way from mixed series of adult and subadult dentitions, rather than on adults alone, which sometimes form less than half the available material and would certainly yield less accurate estimates. The range and mean of the molar crown areas expressed as a percentage of that of the corresponding first molars are: M^1 (100); M^2 97-114 (106); M^3 63-95 (78); M^4 20-49 (31). In the mandibular series, the declension in size is less rapid. The sequence $M_2 > M_3 > M_1 > M_4$ holds for approx. 62%, $M_1 > M_3$ in 31% and $M_1 = M_3$ in the remainder; M_2 and M_4 are constant in the sequence. The variation in crown area of the lower molars and their mean values, expressed as a percentage of that of M_1 is: M_1 (100); M_2 113-134 (124); M_3 90-121 (104), and M^4 40-60 (49).

With regard to size relation between the upper and lower series there is also much overlapping, but in general the upper 1st and 2nd molars are larger in crown area and relatively wider than the lower and the lower 3rd and 4th molars are larger in area and wider than the upper. Length > breadth is the commoner condition in most of the molars of both series, but breadth > length has the higher frequency in M^1 , M^2 and M_3 . In M^1 the posterior lobe is generally

wider than the anterior, and in M_1 invariably so; in all other molars both upper and lower, narrowing of the posterior lobe is by far the commoner condition. M^4 is excessively variable and sometimes almost vestigial and is not always strictly bilobed in form, so that its quantitative relations are less accurately expressed than in the anterior teeth.

The crown pattern of the molars is essentially similar to that of *Caloprymnus* and *Acypyprymnus* and represents an advance on the lophodont element of the bunio-lophodont system of cusps which prevails in the rest of the sub family. In the upper molars, however, the main transverse ridges are still confined to the buccal cusps. There is a general increase in height and saliency of all cusps and ridges and in particular a precursor of the anterior basal ledge of the Macropodinae is strongly developed. In unworn upper molars, the occlusal surface is narrow, occupying only about $\frac{1}{2}$ the available width of the crown, and the exposed lingual wall is frequently twice the height of the buccal. Corresponding features in the lower teeth are similar but less marked. Crown wear on the molars is comparatively slow and at the P^4 M^4 stage dentine exposures are generally confined to the lingual cusps of M^1 ; in very aged examples it does, however, proceed to complete obliteration of crown pattern. Interproximal wear is also negligible except in very aged examples. In the three dimensions studied there is no significant difference between corresponding molars of adult and subadult dentitions.

The range and mean (in brackets) for—(1) the antero-posterior length; (2) breadth of anterior lobe; and (3) breadth of posterior lobe, of the molars in a bisexual series of 15 skulls, follows:— M^1 , 4.0-4.4 (4.2); 3.9-4.5 (4.2); 3.9-4.6 (4.3). M^2 , 4.0-4.5 (4.2); 4.1-4.7 (4.5); 4.0-4.6 (4.2). M^3 , 3.6-4.0 (3.8); 3.6-4.2 (3.8); 3.0-3.5 (3.2). M^4 , 2.0-3.0 (2.3); 2.1-2.8 (2.3); 1.5-2.2 (1.8). M_1 , 3.7-4.2 (4.0); 3.0-3.6 (3.4); 3.6-4.2 (3.8). M_2 , 4.0-4.9 (4.4); 3.9-4.5 (4.1); 3.8-4.5 (4.0). M_3 , 3.6-4.1 (3.9); 3.7-4.2 (4.0); 3.0-3.8 (3.5). M_4 , 2.4-3.1 (2.8); 2.6-3.0 (2.8); 1.6-2.2 (2.0). The values for Ms_{1-3} in situ are: Upper 11.4-13.0 (12.1). Lower 11.3-12.8 (12.2).

The tooth change in *B. lesueuri* is subject to considerable variation; the commonest condition is that P^4 erupts after M^3 or with M^4 , when the skull has attained to 90% of its metrical development and somatic development is equally advanced. The premolar condition in *B. lesueuri* is a more reliable guide to maturity than the molar; M^4 is erratic in coming into place, sometimes delayed until the skull is

aged, at others appearing precociously in very early life. The functioning dental condition P^3M^3 appears to be long persistent and tides the animal over a considerable range of developmental stages.

Sexual differentiation in the teeth is chiefly shown by the 1st upper incisor which in both adult and subadult groups is distinctly larger in males than in females and of more persistent growth. In this it usurps the usual sex linkage of the canine, which is not appreciably different in the sexes.

THE LOWER SOUTH AUSTRALIAN REPRESENTATIVE.

DISTRIBUTION AND HABITS: There is abundant evidence to show that *Bettongia lesueuri* was formerly one of the most numerous and universally distributed mammals of South Australia, finding and colonizing suitable habitat zones in all the districts of the State with the possible exception of the deeper Mallee and the flooded portion of the lower South-East and the inner portions of the Nullabor Plain. It was well established on the Adelaide Plain, where its remains are sometimes brought to light today from long forgotten warrens, by suburban building operations.

To the early settlers it was a familiar animal and traditional knowledge of it persists in many country districts, but written accounts are rare, the early press commentators on the South Australian fauna nearly always quoting the existing accounts of Waterhouse and Gould, which relate almost entirely to Western Australia. A valuable exception was provided by A. Molineux who published some interesting details of its abundance in 1855-6 in the farming districts of the Lower North between the Light and Gilbert Rivers, 50 miles north of Adelaide, where it did some damage at harvest time, both to standing crops and hay stooks. He mentions having shot 149 in four nights, and 50 in one night in this locality, and confirms much that had been observed by Gilbert in Western Australia; particularly in the enormous size of the warrens, the call, and the strictly nocturnal habit. He considered that they were grass and grain eaters in the main, and referred to the European prejudice against the flesh, which he had personally found baseless. J. H. Browne (1897) also gave a valuable account of it in the same district, describing its burrows and the natives' method of procuring it therefrom which included a fumigating technique as in the Centre.

G. W. Francis records that in 1862 it was one of the first zoological items in the collection maintained in the Botanic Gardens,

as an early precursor of the Adelaide Zoological Gardens, and two years later M. Symons Clarke gave details of two specimens taken near the suburb of Walkerville, and again in 1889 near Two Wells, 30 miles north of the town. From 1900 to 1904 the greater number of the specimens in the South Australian Museum were received, chiefly from the Gawler River district, which at this time, was one of its last strongholds on the Adelaide-Wakefield Plain. A small group from this locality was maintained in captivity in the Museum grounds, and formed the basis of the mounted group now exhibited there. The last specimen from Eyre Peninsula was obtained at Worunda, near Port Lincoln—the locality of Waterhouse's type of *harveyi*—in 1909.

With regard to aboriginal names for the species in lower South Australia, the only terms which can be assigned to *lesueuri* with much certainty, are *yelki* of the Narranga of Yorke Peninsula, and *bukurra* or *bokra* of the Ngadjeri of the Lower North district.

The chief causes of its remarkably sudden decline have been discussed by Wood Jones (*op. cit.*), but these are not adequate for a complete explanation in all districts. The late Mrs. Daisy Bates while at Ooldea collected considerable evidence from the aborigines to show that its numbers had diminished markedly in the coastal areas at the Head of the Bight before European influence had become appreciable there, and this at a time when it was still very plentiful in the drier tracts north of Ooldea to the Musgraves. However, by 1910 from one cause or another, it appears to have been virtually extinct in the Southern Division of the State, below the parallel of 32° South, which includes all the agricultural areas. In the pastoral country to the north of this line, the succeeding 40 years have, as far as can be ascertained, seen its disappearance from all except the far north-western district, where both its populations and its prospects of survival are identical with those of the Centre, already reviewed.

We owe to the energetic intervention of the late Professor Wood Jones the possibility of the survival of the species in the south. In 1920 he obtained living specimens from the Lake Phillipson area in the north-west division, and successfully maintained them as a breeding colony at the University of Adelaide for some years. Some of the progeny of this group were transferred in 1924 to the sanctuary of Flinders Chase at the western end of Kangaroo Island at the mouth of St. Vincent Gulf. The site is for the most part densely bushed and not very well suited to its habits, but recent reports from the Ranger indicate that it is still extant though its increase is slow.

Reports of the recurrence of "kangaroo rats" in the southern mainland of South Australia, are made almost yearly, but all which have been investigated prove to be due to confusion with the bandicoot, *Isodon obesulus*.

Remains of the species are plentiful in alluvium and cave deposits throughout the State and are a common constituent of aboriginal kitchen middens.

The series examined below represents approximately 36 individuals, of which the bulk is unsexed skeletal material. It is much more restricted in geographic range than the Central Australian collection, coming for the most part from the coastal Adelaide-Wakefield Plain, with outlying specimens from the nearer foothills of the Mt. Lofty Range and from Yorke and Eyre Peninsulas. The locus of its most northerly specimens is 700 miles south-west of that of the most southerly of the Central series. Some examples bred in captivity by Wood Jones from stock from Lake Phillipson, an intermediate site, are anomalous in respect to pelage and cranial characters and have been deleted from both accounts.

EXTERNAL CHARACTERS AND PELAGE can be tested only on four individuals; a skin from southern Eyre Peninsula and three mounted specimens from the Adelaide district, which have been on exhibition in the South Australian Museum for thirty years. Soft parts, so far as they can be checked in this dried material are in close agreement with the Central animal. The Eyre Peninsula skin is in good preservation, unfaded and indistinguishable from winter skins from the Centre. The mounted specimens are too faded for colour comparisons, but are in close agreement with Central skins in all points of composition and colour distribution; the subadult specimen has a white apical crest strongly developed. The pelage is not richer in the south.

FLESH DIMENSIONS are quoted in the table on p. 267 for a bisexual series of 9 examples at P⁴M⁴. The variation is still wider than in the Centre, reaching 26% in the head and body length, and there is a wide overlap with that series in each item; the slight increase in the mean length of pes in the south may be significant, but the other differences are doubtfully so.

CRANIAL CHARACTERS (Pl. xxvii, fig. C): Twenty skulls from Lower South Australia have been examined and measured; four only are subadult, the remainder are at P⁴M⁴ and for the most part are much more aged than skulls of the same dental stage from Central Australia.

In structural features there is close agreement with the Central series but the southern skull tends to be slightly larger. In a series of 21 cranial and mandibular measurements of the 16 at P⁴M⁴, the increase in the mean value varies from 1 to 15% with an average increase of 5%; the greatest being the length of the anterior palatal foramina (15%), depth of mandible (13%) and diastema (11%). Two other measurements are lower; the least width of nasals (2%) and the facial index (4%). The increase is greater in longitudinal dimensions than in transverse, so that the skull is frequently proportionately narrower in zygomatic width (8%) and in the width of the mandible and its condyle (9%).

The differences between the two geographic series have no doubt been accentuated by the greater average age of the lower South Australian skull, but are not primarily due to this cause, since the subadult skulls at P³M³ show similar differences from their Central counterparts. The mean variation in the dimensions of the southern series is even greater than in the Central one, in the proportion of 22-15, and in nearly $\frac{2}{3}$ of the measurements the range completely overlaps both maxima and minima of the latter. As in the Central series dwarf fully adult skulls occur, smaller in most dimensions than average subadults.

DIMENSIONS: The following figures give the range and mean of skull measurements of bisexual groups of (1) 16 at P⁴M⁴ and (2) 4 at P³M³. Greatest length, 63.2-76.2 (72.9), 68.0-70.0 (69.3); basal length, 54.0-66.5 (63.1), 57.1-60.0 (58.9); zygomatic breadth, 39.5-46.2 (43.9), 41.8-43.2 (42.4); nasals length, 23.3-30.0 (27.8), 24.7-25.7 (25.3); nasals greatest breadth, 11.5-15.3 (13.2), 10.0-11.9 (11.1); nasals least breadth, 5.0-7.0 (5.8), 4.6-5.5 (5.1); depth rostrum, 11.5-14.1 (13.3), 11.7-13.6 (12.7); interorbital constriction, 14.0-17.0 (15.5), 14.6-15.2 (14.9); palate length, 33.3-41.2 (38.7), 34.0-37.5 (35.9); palate, breadth inside M², 10.3-13.3 (12.5), 10.8-11.8 (11.3); ant. palatal foramina, 2.5-4.4 (3.3), 2.7-3.2 (3.0); diastema, 6.7-10.2 (8.7), 7.7-9.0 (8.2); bulla length, 14.6-18.7 (17.1), 16.0-18.0 (16.7); bulla breadth, 10.5-14.8 (12.6), 12.4-13.5 (13.0); facial index, 162-195 (174), 171-181 (174); mandible, maximum breadth, 38.0-45.0 (42.4), 40.5-40.5 (40.5); mandible, depth below M₂, 9.0-11.8 (10.3), 8.1-9.2 (8.7); mandible, breadth ascending process, 13.4-17.0 (15.0), 14.0-14.4 (14.2).

DENTITION: Here also the range of variation in dimensions is greater than in Central Australia, and in all items there is a generous overlap between the two series. The mean dimensions of teeth which

are substantially free from age and wear changes, such as the length and breadth of premolars and molars tend to be slightly higher than in Central Australia, the chief increases being P^4 3.5%, P^3 6%, Ms^{1-3} 3%, M_{1-3} 4%, M^4 15%, M_1 10%. In many other dimensions, however, there is a virtual identity of mean values and P_3 is 2% and M_1 4% lower. The prediastemal teeth are difficult to compare accurately owing to age changes, but in subadults are also slightly larger, the canine probably as much as 10%.

Structurally the teeth in the two series are in close agreement. The crown of the canine is obscurely bicuspid in two examples. P^4 is somewhat more constant in talon development than in the Central series and its anterior expansion is more frequent and more marked; one 7-grooved example occurs, but otherwise 8, 9 and 10 grooves appear with about the same frequency as before. In the lower P_4 a taloned variant with sigmoid outline (Pl. xxviii, fig. J) not seen in the Central series, occurs in 2 examples.

The chief change in the absolute dimensions of the molars as compared with their Central Australian counterparts, is the mean increase in the 3rd and 4th of both jaws, and of the 2nd in the upper, and a decrease in M_1 of the lower jaw. The molars also tend to be slightly narrower.

The gradation in molar size as interpreted by the sectional crown area yields the same prevailing sequences as in the Central material. The enlargement of the posterior teeth with respect to the first however (especially marked in the lower jaw), leads to the occasional appearance of such conditions as $M^3=M^1$ and $M_3=M_2$, which have not been noted in the Centre, while $M^1>M^2$, $M_1=M_3$, and $M_1>M_3$ do not occur. In the upper molars $M^2>M^1>M^3>M^4$ accounts for approx. 90% of the cases, $M^2>M^1=M^3>M^4$ for 5% and $M^2=M^1>M^3>M^4$ for 5%. In the lower series $M_2>M_3>M_1>M_4$ occurs in approx. 79% of cases and $M_2=M_3>M_1>M_4$ in the remainder. The range and mean of the sectional crown areas expressed as percentages of those of the first molars, are as follows: M^1 . (100); M^2 . 100-125 (112); M^3 . 68-100 (83); M^4 . 27-59 (36) and M_1 . (100); M_2 . 117-142 (130); M_3 . 104-132 (119); M_4 . 53-82 (62).

The tooth change is not illustrated. There are no supernumary molars, but a vestigial I^4 occurs in one example. The following figures give the range and mean of the linear dimensions of the cheek teeth; the values for the third and the deciduous premolars are derived from 4 subadults and the remainder from 16 at the P^4M^4

stage. P^1 length, 7.7-9.3 (8.5); P^1 breadth, 2.6-3.6 (3.1); P^3 length, 5.0-5.6 (5.3); P^3 breadth, 2.6-3.0 (2.8); MP^1 length, 3.4-3.7 (3.5); MP^1 breadth ant. lobe, 2.8-3.1 (2.9); Ms^{1-3} *in situ*, 11.3-14.0 (12.5); and in the mandible P_4 length, 6.0-7.5 (6.9); P_4 breadth, 2.5-3.3 (2.7); P_3 length, 4.3-4.6 (4.4); P_3 breadth, 2.3-2.7 (2.5); MP_4 length, 3.2-3.5 (3.4); MP_4 breadth, 2.0-2.3 (2.2); Ms_{1-3} *in situ*, 11.1-13.0 (12.7); M^1 anteroposterior length, 3.9-4.6 (4.2); breadth anterior lobe, 3.7-4.5 (4.2); breadth posterior lobe, 3.6-4.5 (4.2). M^2 , 4.2-5.2 (4.5); 4.0-5.0 (4.4); 3.6-4.8 (4.2); M^3 , 3.5-4.5 (4.0); 3.5-4.2 (4.0); 3.7-4.0 (3.4); M^4 , 1.9-3.6 (2.7); 2.1-3.3 (2.8); 1.7-2.5 (2.1); M_1 , 3.5-4.2 (3.8); 3.1-3.5 (3.3); 3.4-4.0 (3.7); M_2 , 4.0-4.9 (4.4); 3.6-4.3 (4.1); 3.7-4.5 (4.0); M_3 , 3.6-4.7 (4.3); 3.6-4.3 (4.1); 3.4-4.1 (3.7); M_4 , 3.0-3.4 (3.1); 2.7-3.4 (3.0); 1.9-2.8 (2.3).

SUBSPECIFIC DIFFERENTIATION IN *Bettongia lesueuri*.

The relationship of the Central Australian and lower South Australian Populations: While it is possible by the close examination of series to detect and define divergent trends in these two populations, it must be emphasized that the differences noted are not only slight in themselves but are of an average character and leave many individuals of both groups virtually inseparable by an appeal to the minutiae of morphology, and certainly quite inseparable by the facile and subjective methods which have been rife in differentiating geographical "forms" of Australian mammals. It is noteworthy that the range of variation in the geographically restricted sample from lower South Australia is greater in most items than in the more widely dispersed one from the Centre; a fact which appears to conflict with the belief, for which there seems much justification in other cases, that aridity with its concomitant of instability in ecological conditions, is a potent factor in promoting variability in eremian forms.

Under these circumstances the use of another trinomial to distinguish the Central Australian animal is clearly superfluous and for practical purposes the two groups are here regarded as forming a taxonomic unit.

The wider question of the validity of *B.l. harveyi* as a South and Central Australian subspecies, in relation to the typical *B. l. lesueuri* of Shark Bay and *B. l. grayi* of the Swan River district, is beyond the practical scope of the present work. Although large collections of both the latter are in existence and both have been stated to be variable, no detailed analysis of characters has been published, and

without such the material locally available is inadequate for a decision. Tate (1948, 269) the latest commentator, on a basis of existing accounts, opines *grayi* doubtfully distinct from *lesueuri*, *harveyi* probably more so. Cabrera (1919) held the opposite view.

The following comments, suggested by the results of the foregoing examination, are made as an interim contribution on this head. Recent belief in the distinctness of *grayi* from *harveyi*, seems to be based chiefly on the statement of Wood Jones (*op. cit.* 210) that the Western Australian animal was larger bodied and shorter eared. The comparison from which this conclusion arose, appears to have been made between South Australian animals measured in the flesh and the dimensions of the type as given by Thomas (1888) for the stuffed skin, in which the ear would have been much contracted and the body very probably stretched. The more recent measurements of Shortridge in Thomas (1907) made on animals in the flesh from the Avon district of Western Australia give values for the head and body and tail which are much closer to those of South, Central and north-west Australian specimens, while both ear and pes are actually the longest recorded.

The skull characters of the south-western animal have not hitherto been known with certainty; the specimen O measured by Thomas (1888) is doubtfully localized and gives values which merge almost entirely with those of lower South Australia. The provenance of Waterhouse's specimens is also uncertain. Three skulls from south-west Western Australia which have been examined during the present work, differ from the lower South Australian population in much the same way as the latter do, from that of Central Australia, i.e., there is an average 6% increase in the mean of all dimensions except 3; the greatest being in the rostrum which is noticeably deeper and wider and in the least breadth of nasals. The diastema, inter-orbital constriction and breadth of bulla are slightly lower by 2-3%. Again, however, as in the South-Central Australian comparison there is a very wide overlap in the range of dimensions, which involves 20 of the 23 items studied.

Similar size increases occur in most elements of the dentition and there is a slight increase in hypsodontism especially of P⁴ (Pl. xxviii, fig. K) which is a stouter as well as a higher tooth when unworn; its grooves are 10 in the 2 examples which can be counted—Thomas records up to 14 for the species. The mean for the length of molar rows is not increased but the individual teeth are slightly broader than in South Australian skulls. In matters of proportional development

which can be tested by mensuration, the south-western skull and dentition are closer on the whole to those of lower South Australia than to those of the Centre, but in a small residue of characters an intermediate condition obtains. In the crown area ratios of the molars for example, the upper teeth repeat and accentuate the trend in the lower South Australian series, towards enlargement of the posterior teeth at the expense of the first. But in the lower jaw there is a return to the Central Australian condition. The size sequence formula however, for both upper and lower teeth is the dominant one as it occurs in both South and Central Australia.

One only of the 3 skulls examined is accurately localized; this is a large male at P^4M^2 , taken at West Popanyinning, 90 m. south-east of Perth (Pl. xxvii, fig. D). Its dimensions are as follows: greatest length, 76.0; basal length, 66.1; zygomatic breadth, 47.4; nasals, length, 31.5; nasals, greatest breadth, 14.5; nasals, least breadth, 6.6; rostrum, depth, 14.8; interorbital constriction, 14.5; palate length, 41.5; palate breadth inside M^2 , 13.0; anterior palatal foramina, 3.9; diastema, 8.6; bulla, 17.0 x 12.5; facial index, 175; mandible, maximum breadth, 44.0; mandible depth below M_3 , 11.0; mandible breadth asc. process, 17.6; P^4 8.8 x 3.5; Ms^{1-3} 13.2; P_1 7.0 x 3.0; Ms_{1-3} 13.3.

A single skull from Coolgardie, 330 m. east of the Swan River district (in the subarid Goldfields environment) is closer to the means for lower South Australia.

No material of the typical race certainly localized in Shark Bay or the North-West Division of Western Australia, has been examined by the writer, but Shortridge's field measurements (in Thomas, 1907), indicate that the means for Bernier Island specimens are slightly higher than those of Central or South Australia, except for the ear which is equally shortened. Of pelage characters, little can be gleaned except that *vide* Collett (1897) the apical blanching of the tail is less frequent in adults than in South and Central Australia.

The only detailed skull measurements of this typical form available to me are those of Waterhouse (1846, 205) based on a drawing by Owen and doubtfully comparable with the other data. However, as amplified by Collett and Thomas, it would appear that a very small bulla (considerably below the mean in any other group) exists in a comparatively large skull, and if this ratio is constant, it would provide a valid distinction from the series here studied. Collett

TABLE I
EXTERNAL DIMENSIONS OF THE "RACES" OF *Bettongia lesueuri*

	Head and Body	Tail	Pes	Ear
Lower South Australia. Bisexual 9 at P ⁴ M ⁴ . H.H.F....	286-385 (319)	276-330 (301) ²	97-108 (104)	34-37 (35) ¹
Lake Phillipson ♂. F.W-J.	370	300	105	40
Central Australia. Bisexual 8 at P ⁴ M ⁴ . H.H.F.	315-370 (344)	280-305 (293) ²	96-104 (101)	31-39 (35) ¹
Type of "grayi". Stuffed skin ♂. Recalculated ex Gould,	457	292	108 ³	27.5 ⁴
"grayi", Avon district, W.A. 1 ♂, 1 ♀, ex Shortridge	360-390 (375)	285-310 (297)	108-112 (110)	40-42 (41)
"lesueuri", Bernier Is., W.A. 1 ♂, 1 ♀, ex Shortridge	350-360 (355)	280-300 (290)	102-110 (106)	35-36 (35.5)

¹ From tragoid notch.

² From cloaca.

^{3,4} Quoted by O. Thomas in *B. M. Catalog.* as 103 and 29 respectively.

mentions also a sagittal crest and a bicuspid canine; the former has not been noted but the latter occurs sparsely in South Australian skulls.

In taking a general view of the inter-relationships of the material reviewed, it is clear that, in cranial and dental characters at least, the three populations of *Bettongia lesueuri* in Central, South, and the south-western portion of Western Australia, form a metrical cline ascending in the sequence named, but with a wide overlap between succeeding groups. At each stage of the transition a few characters may be found to provide examples of lag or even reversion, but abrupt discontinuities, of a kind foreshadowing speciation, are not presented.

***Bettongia penicillata* Gray 1837, subsp.**

DISTRIBUTION AND HABITS: The presence of this species in Central Australia has not hitherto been recorded; Le Souef indeed (1926) expressly excludes it therefrom in his remarks on its distribution.

In 1932, Mrs. D. Bates at Ooldea, drew my attention to an aboriginal myth based on the karpitchi, an animal described as resembling *Caloprymnus* in size and appearance, in sharing also a nestmaking habit, but differing in its black brushed tail. A year later, in the Everard-Musgrave Range district, I learned that the karpitchi was a living entity and known by that name, both to the original Yankunjarra and to the Pitjanjarra, who partly supplanted them from the west. They compared it with the tchungoo or metika (*B. lesueuri*), but confirmed the nestmaking and black caudal crest, and knew it as a sparsely occurring animal over a considerable area straddling the South and Central Australian border. In the next two years it was reported from Pundi (the most southerly point, about 85 miles south-west of Ernabella), at Unyaba Hill on the Officer Creek, at Mount Harriett, where a specimen was taken which was kept for a time by a white dogger as a pet, and near Mount Conner, approximately 70 miles west of north of Ernabella, on the Central Australian side. In none of these cases was I able to examine any material, but in the old collections of the South Australian Museum is a specimen taken near Waldana Spring, about 125 miles north-west of Ooldea, and this is the only example of the karpitchi here studied.

The species is also recognized by aborigines from specimens, and substantially similar accounts given of its habits, over large areas of the eastern and north-eastern parts of the Territory, where it has long ceased to exist. In the hill country of Huckitta the Ilyowra called it

indwarritcha; to the Worgaia on the Buchanan and Rankin Creeks it was windijarra, and probably the yelkamin of the mixed Warramunga and Walpari people east of the Murchison and Devonport Hills. North of the Barkly Tableland along the Gulflands both in Queensland and the Northern Territory it is probably still extant, and groups of mixed Alowa and Mara blacks from Tanumbirini and Nutwood, recently gave it the name, yamul. Elsewhere in the north there are but vague accounts of it at Mainoru, at the Katherine and possibly in the Finnis River district; but it may be noted that the vast areas of richly grassed eucalypt savannah south of the Arnhemland plateau, would by analogy with its habitats in the south, provide ideal stations for the species, but for the presence of stock.

In the winter of 1933, Michael Terry, while prospecting on the Western and Central Australian border, observed "spinifex rats" of which he has given some account in his book "Sun and Sand." This account, however, has a three species basis, involving *Lagorchestes asomatus*, *Lagorchestes hirsutus* and *Bettongia penicillata*. Among specimens sent by him to the South Australian Museum is a portion of a skull from an animal taken in July 1933 near the McEwin Hills in the Lake Mackay area about 470 miles north of the Waldana site, and in the sequel this is treated tentatively as a second and markedly distinct eremian phase of *B. penicillata*.

DISTRIBUTION ELSEWHERE IN AUSTRALIA: Much uncertainty prevails as to the former extent of the distribution of *B. penicillata* in Australia, with some conflict in existing accounts. While it is no longer possible to ascertain the full truth, a review of records State by State, will fill in other gaps than the Central and Northern Australian one, and clarify some obscurities.

Western Australia: The work of Shortridge (1910, and in Thomas 1907) and of Glauert (1933, 1950) has made the position clearer here than in the East. The northern record is at Shark Bay, whence it extended in a widening belt to the Pallinup River on the south coast. East of this line it is also accorded some tenure by these authors, but the extent of it is vague and leaves the question of linkage with the south and central populations unsolved. However, the Central Australian records given above are sited in eremian conditions much more severe than those of its presumed eastern frontier in Western Australia and go far to support the existence of such links, if not today, at least in the recent past.

South Australia: The early writings of Gray (1843), Gould (1852), Harvey (1840) and Waterhouse (1841) establish it on lower

Eyre Peninsula, at the head of St. Vincent Gulf and in the Adelaide district. Later, rural tradition following its extirpation, gives it a very wide, if not universal distribution over the southern parts of the State. It is less easy to trace in this way than *B. lesueuri*, however, and was sometimes confused with *Lagorchestes leporoides*, but when both bettongs were known, *B. penicillata* seems to have been the commoner species. Mainland records for South Australia supported by recent material locally available are limited to a few examples in the South Australian Museum (*infra*) which come from the west slopes of Mount Lofty and from Waldana, but sub fossil and native camp site specimens, many of the latter quite recent, confirm its presence in the lower South-East, the Fleurieu Peninsula, Murray Mallee, and Yorke Peninsula.

North of the 32° parallel, there are neither material records nor accounts which can be regarded as free from entanglement with *Lagorchestes*, except those of the Waldana and Musgrave-Everard Range area in the far North-West, noted under Central Australia. The karpitchi legend is not local to Ooldea but derived from visitors from the Musgraves. In spite of this wide hiatus in records in the subarid areas of the State, the Musgrave-Waldana occurrences support the view of a former complete north-south occupation of South Australia, as in the case of *B. lesueuri*, though it cannot be supported by evidence as with that species. At least one, possibly more insular representatives occurred in South Australian waters. A skull of the extinct St. Francis Island bettong has been examined (*infra*) and proves to be a form of *B. penicillata* as predicted by Wood Jones; and the "kangaroo" smaller than a cat, taken by Flinders' party on Flinders Island in 1802 (Cooper 1953) may also be referable to this genus. However, Flinders' accounts of the small macropods of these islands, like those of Baudin, Peron and Ronsard (Cooper 1952) are evidently a blend of *Thylogale eugenii* with smaller forms.

Extirpation of *B. penicillata* in South Australia appears to have followed much the same course as with *B. lesueuri*; the last three examples taken, of which I have been able to get reliable accounts, were at Riverton in the Lower North district in 1908, at Lameroo in the Murray Mallee in the same year and on the Wild Dog Creek in the Fleurieu Peninsula in 1910.

Of the several aboriginal words which have been applied to "kangaroo rats" in lower South Australian vocabularies, only one, the coolgar of Harvey (1840) at Port Lincoln on Eyre Peninsula can

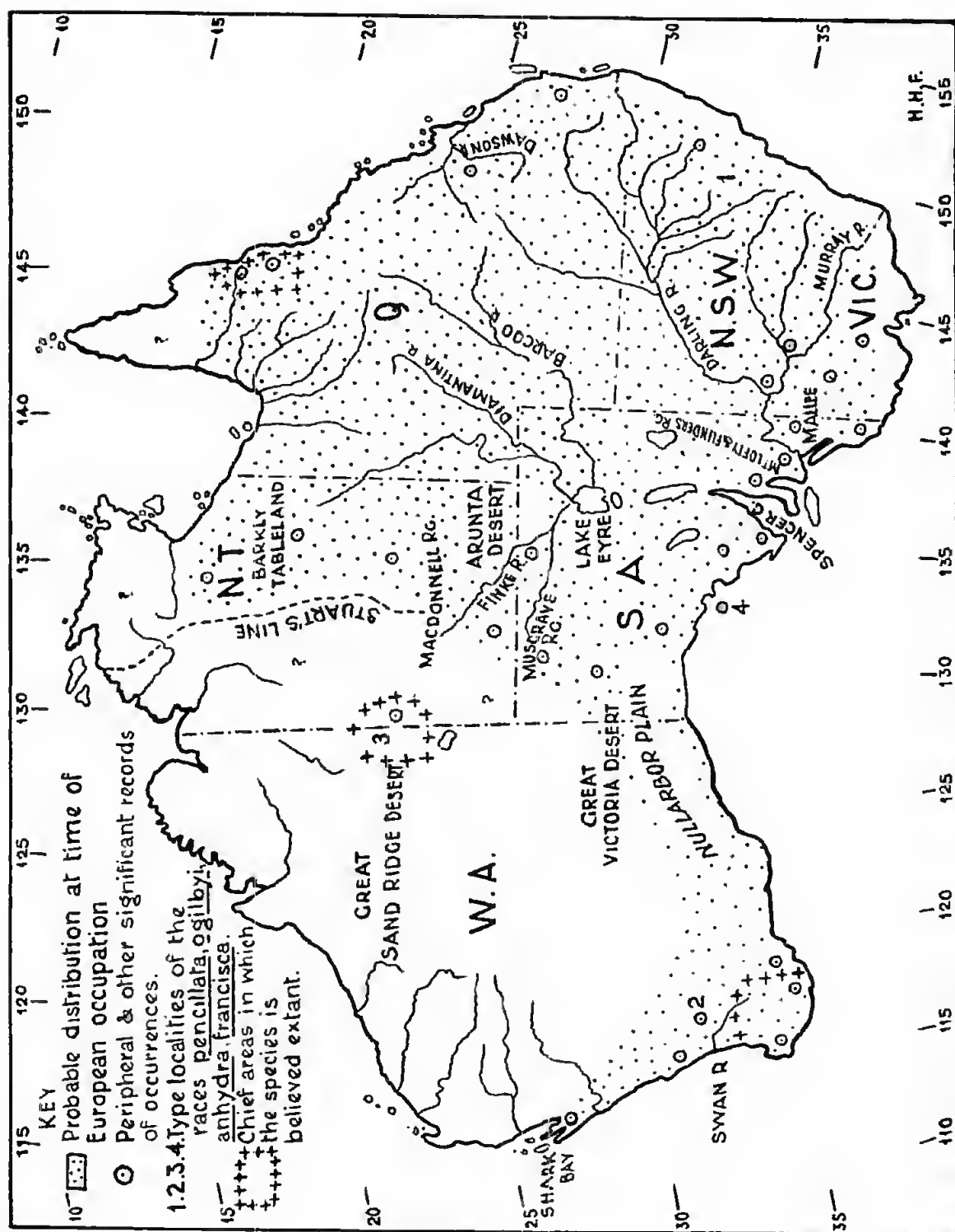


Fig. 2. Map of the distribution of Bettongia penicillata. Gray.

be applied with certainty to *B. penicillata*, the animal so-called having been identified by Gould in 1853. This is clearly equivalent to kulka of the later Parnkalla vocabularies of Eyre Peninsula and probably also to koka and kurka of the Kaurra of the Adelaide district. The names bukurra or bokra of Le Brun and Browne's providing, have been linked with *B. ogilbyi* (= *penicillata*) by Johnston (1943) but definitely belong to the burrowing species, *B. lesneuri*.

Victoria: There are several categorical and inclusive statements of the occurrence of *B. penicillata* in Victoria, viz., Forbes Leith and Lucas (1884) and Thomas (1888), but the extent of its occupation is uncertain. Brazenor (in Harper 1945) states that Victorian specimens are in the National Museum, Melbourne, and that the last record was in 1857. Later, however (1950), he omits *B. penicillata* from the list of Victorian mammals and substitutes *B. cuniculus* Ogilby, hitherto regarded as exclusively from Tasmania, where *B. penicillata* does not occur.

I have accounts of a nest building bettong from West Victoria generally in 1854, and the Grampians district in 1910. Nest building would not of course distinguish *B. cuniculus* from *B. penicillata*, but the South Australian populations in the lower South-East and Murray Mallee districts were almost certainly continuous into Victoria, and they are based upon a form with a small rounded extraverted secator, quite different from that of *B. cuniculus*.

New South Wales: The chief sources here are Gould and Krefft. The former (1841.1852) had personal knowledge of it down the course of the Namoi to its junction with the Gwydir and on the adjacent Liverpool Plains. He accorded it also a wide distribution throughout New South Wales except for the coastal slopes of the Divide, where he considered it to be replaced wholly or in part by *gaimadi*, held by some to be a closely related, possibly subspecific form. Krefft (1864) recorded it in western New South Wales on the lower Murray between the Darling junction and Euston, 60 miles south-east, and made the interesting statement that at Gunbower Creek, 150 E. of Euston, it is completely replaced by *Aepyprymnus*. He does not mention *B. penicillata* on the Victorian side of the river.

Queensland: The species is not listed for Queensland in any of the earlier accounts, and until quite recently, localized records were limited to the original one at Coomooboolaroo in the Dawson Valley. This was based upon the personal testimony to the writer of Charles Barnard (a well informed naturalist and son of Luniholtz's host), who

contributed largely to the latter's collection. W. Boardman (1943), however, published on an example from Pine Mountains in south-eastern Queensland (Aust. Museum Sydney, No. 1121). Three localities are so named in this area, and which is relevant is not known—a mean position for it is plotted on the distribution map. Tate (1948, 267 and 1952, 592) has given details of seven more in American museums, taken at Mount Spurgeon and Ravenshoe towards the western fall of the Atherton tableland; three of these were taken as late as 1932. Recent enquiry by the writer in the field suggests that it may still survive in the Gulf country of the north-west of the State adjoining the Northern Territory border, though no material is available in support.

The overall range of *B. penicillata* as outlined above, was probably as extensive as that of *B. lesueuri*. While it was absent from a considerable north-western sector occupied by the latter, its eastern and north-eastern extension was much greater, and this, containing the chief highlands of the country, adds much to the total diversity of habitats occupied. The Torresian occurrence is noteworthy as its northern extension nearly equals that of *Aepyprymnus rufescens*, which belongs exclusively to the east coast lands. Thomas' dictum of 1888, on the range of *B. penicillata* "all Australia except the extreme north" seems to have been at that time an expression of opinion rather than an ascertained fact, but in the sequel as developed above, it comes near the truth (fig. 2).

The status of the species is even more insecure than that of *B. lesueuri*. Probably $\frac{1}{10}$ ths of its former range is now empty of it and it survives only in three widely separated localities of North Queensland, the Western Centre, and the south-west of Western Australia. Its hold in the two former is slight and in the latter alone does there seem much hope of perpetuating it.

HABITS: The sites which furnish the above records present ecological contrasts of an extreme kind. They vary from North Queensland forests under a 50in. rainfall, to spinifex plains on the edge of the Sandridge Desert; from coastal dunes in Western Australia to 5,000ft. plateaux in New South Wales; and from thermal constancy under the monsoon in the north to marked seasonal changes and sharp winters in the south-east. Moreover, versatility in exploiting habitats is shown not only on this regional scale but in the frequently ubiquitous nature of its occurrence in restricted areas. In South Australia it was less selective in this regard than *B. lesueuri*.

and occurred in the Mallee and in the higher stringy bark (*Eucalyptus obliqua*) tiers of the ranges, where the latter was rare or absent. On the Fleurieu Peninsula, much favoured nesting sites were the patches of blue gum forest (*Eucalyptus leucoxydon*) with a wiry tussock sedge (*Lepidosperma carphoides*) and sparse herbage on an otherwise rather open floor. At Cuballing in the south-west of Western Australia where in January 1926 I obtained part of the series examined below, a rather similar plant association occurs in Wandoo forest (*Eucalyptus redunca* var. *elata*); but here the terrain is varied with rocky ridges supporting thickets of a prickly shrub, *Dryandra nobilis*.

Nest making appears to be very characteristic of the species and in some form or another is exhibited in all types of country even in the spinifex flats of the Centre. But nests are not the only form of camps used; in Western Australia it is sometimes locally very abundant, as Shortridge records for Pingelly in 1904 and as I found it at Cuballing, where the animal was much more numerous than its nests in the quite restricted areas from which it was flushed. It is probable that at such times a proportion shelter in hollow logs and rock cavities on the *Dryandra* ridges. The type of nest made evidently varies somewhat with locality; Gould's account from New South Wales differing considerably from Gilbert's in the Swan River district of Western Australia. I have seen no examples in South Australia but they are described by those who knew them both here and in western Victoria, as rounded and woven of grass stems and there is no mention of the earth excavation at the base as in New South Wales nor of the use of sticks in place of grass and of a tubular entry porch as in Western Australia.

At Cuballing, those put up in the day time from grassy flats had a characteristic somewhat unwallaby-like gait with the head low, back much arched and the tail not rigidly curved but fluent and with the black brush displayed very conspicuously—it did not seem at all fast, under these conditions. Wood Jones records that it was used in coursing in South Australia under the name "Squeaker"; but this term was also applied in South Australia to a hare wallaby *Lagorchestes leporoides*, whose speed and saltatory powers were exceptional. In the evenings they were constantly about the enclosure at the homestead, and even when invisible could often be located by their soft grunting in the dusk. By means of freshly toasted bread they were enticed up on to the verandahs, where they were not at all abashed by the presence of three people, several cats and a lighted lamp; cats and bettongs were often within a few feet of one another

and neither animal showed the slightest interest in the other's presence. They were taken very easily in a crude form of box trap improvised for the purpose and baited with toast. Indeed it was often easier to get the animals into the trap than to take them out alive, for if less fierce than *B. lesueuri*, they are exceedingly quick and nimble and bite and struggle as the latter does, with remarkable strength. It shares with *B. lesueuri* and with most of the subfamily the phalangeroïd characteristic of a tender pelage, and large patches of fur and epidermis are easily lost in such encounters. A South Australian observer, M. S. Clark, stated that a local example taken in 1864 showed some slight prehensile power of the tail; I was not able to confirm this with living animals at Cuballing—either in the open or when trapped, but I am not prepared to follow Shortridge (1910, 821) in discounting either its ability, or habit, of carrying grass with the tail for nesting purposes. Gould's positive statements on the matter were apparently based on his own observations and were subsequently confirmed by animals in captivity. Photographic evidence of the same habit in *Potorous tridactylus* is provided by Le Souef (1926, Pl. 54).

Data on reproduction in the field is scanty; a female in my collection taken in July at Augusta in the extreme south-west of Western Australia, had a large furred pouch young of head and body length 210mm. D. L. Serventy (1953-55), who has given an interesting account of his observations in the same district as my own, records large pouch young at the end of March. These two records seem to indicate that the very rapid increase of its populations, which used to occur in Western Australia, were due to the species breeding several times in the year as Krefft (1862) suggested was the case with *B. lesueuri*. Krefft observed only single young in the pouch in New South Wales.

At Cuballing, the living animal was observed to have a strong and somewhat unpleasant smell. No ectoparasites were noted but ova of such were present in the fur.

RECENT MATERIAL OF *B. penicillata* EXAMINED: This is both less plentiful and more diverse than in the case of *B. lesueuri*. 1. For the characters of *B. penicillata ogilbyi* I have relied chiefly on 7 skins and skulls in my own collection, taken at several points in south-west Western Australia and fully authenticated, supplemented by 2 skins and 6 skulls in the South Australian Museum collection and believed to be of local origin. 2. The *Waldana karpitchi* (*supra*) in alcohol.

3. A markedly dwarfed skull of lower South Australian origin. 4. The holotype of *B. penicillata francisca* Finlayson. 5. The holotype of *B. penicillata anhydra* Finlayson.

***Bettongia penicillata ogilbyi* Gould**

EXTERNAL CHARACTERS: Authentic material illustrating the external characters of the species, is available chiefly from Western Australia, and the following brief review is based on dried material representing 7 individuals from Cuballing, Popanyinning, and Augusta in the south-western district and is provided to parallel that of *B. lesueuri* (supra) and to draw attention to the marked variation in pelage which occurs there.

B. penicillata has been said to be the smallest of the genus, but the material in hand indicates that at comparable dental stages it is as large or larger, than the Central Australian *B. lesueuri*. In life the animal appears slighter and more trimly built than the latter, and its limbs are even more delicate, and tail, pes and ear, are all shorter in comparison to head and body length. The head is narrower, the ear broader at base and the upper lip less developed than in *B. lesueuri*. The mien is bold, alert and impish; characteristic of the genus and differing widely from the prevailing types of physiognomy in the Macropodinae (Pl. xxxi).

The upper margin of the naked tessellate rhinarium is produced upwards and backwards in the centre as a more or less acute spur. The mystacial vibrissae reach 40 mm. in length; the lower rows pale brown or whitish, but the remainder jet black; the genals and supra-orbitals, reaching 37 mm., are also black and less developed than in *B. lesueuri*. Eye lashes are weak, as is general in the subfamily, but crescentic rows of stout bristles (to 15 mm.) are strongly developed on the lower margin of the orbit and less so upon the upper. Of submentals and interramals few have survived undamaged in the material—these are colourless and transparent, and in the latter group, reach 12 mm. only.

The manus is similar in its main features to that of *B. lesueuri* but is somewhat longer and slighter and with longer digits and claws. The second digit is longer in relation to the third than in that species, but the digital formula is the same, and the thickening of the fourth digit is carried still further. The claws are yellowish white, have moderate curvature, are laterally compressed and taper little to the apex, in a superior view. The maximum length of the third claw is

14.5 (as against 11 mm. in *B. lesueuri*); the fourth claw is little inferior to the third. The palmar structures are not well shown. Of brachial vibrissae only the ulnar carpal has been seen; a colourless bristle of 12 mm.

The pes is also more slender than that of *B. lesueuri*, but agrees with it in the hairing of the plantar surfaces, which involves the same areas but is less dense; in this it differs markedly from *B. cuniculus* and *Aepyprymnus*, and also from Waterhouse's plate (1846, Pl. 12, fig. 5), which, however, may be based on an abraded example. The granulation of the sole is finer, averaging 19 per cm., and the colouration of integument and nails, though variable, is generally darker; in the darkest examples the sole is nearly black and the nails dusky brown, in contrast to the pale manus.

DIMENSIONS: Published dimensions of the species appear to have been derived chiefly from processed skins and are for the most part uncorrelated with maturity data; the pes measurements also are partly vitiated by inclusion of the nail.

The following are the conventional measurements in mm. taken in the flesh from two advanced subadult males (P^3M^3) at Cuballing: head and body, 330, 305; tail, 261, 279; pes, 107, 104; ear, 38, 38. In an adult female (P^4M^4), the pes reached 110 mm. The percentage relations to the head and body length in these two subadults, as compared with Central Australian *B. lesueuri* at the same dental stage, are respectively: tail, 79-91 (85), 100-122 (108); pes, 32-34 (33), 35-41 (37); ear, 11-12 (11.5), 13-14 (13.3).

PELAGE: This presents much of importance which does not emerge in existing accounts. In the adult unworn pelage the texture is variable; often crisp or even harsh as in *Aepyprymnus* and quite unlike *B. lesueuri*. Mid-dorsally the main pile of under fur, which is copious, reaches 20 mm., with guard hairs to 32 mm., and the length does not increase much elsewhere. The basal $\frac{3}{4}$ of the under fur is about blackish-plumbeous of Ridgway, followed by a subterminal band of snuff brown deepening to clove brown and black on the points. The guard hairs are profusely developed and the majority reach 26 mm.; the banding is the same as in the underfur, except that a narrow zone of dark brown separates the basal grey from the flattened subterminal segment, which is much lighter in colour, near cinnamon buff. A considerable proportion of guard hairs (much higher than in other species) are black throughout their length and more strongly flattened; they are so numerous as to constitute almost a third pile

reaching 32 mm. in length. The general dorsal colour is a rich grizzled brown near snuff brown and is determined by the admixture of brown, buff and black of the terminal and subterminal bands, the basal grey being entirely excluded from the surface. It is uniform over the head, body and limbs, the tail alone contrasting in darker and richer tones.

The sides are slightly paler; there is no lateral line of buff but a gradual transition to the ventral colour, which is greyish white washed with cream buff; areas of pure white are sometimes present on mid line of belly and throat. The muzzle is brown (near bistre) and not grizzled, the rest of the head like the back. The ear backs are well furred, snuff brown to the base and not grizzled nor darkened at margins and little contrasted with the crown; the inner surface sparsely clothed and somewhat lighter than the backs; the tuft at the tragoid notch, inconspicuous.

The manus and digits are well haired but the nails are not obscured. The colour variable; basally a deep brown, but bleaching irregularly on the surface to grizzled clay colour; the digits pale drab or near white. The pes also well haired and strongly fringed, the terminal bristles on fourth toe reaching 25 mm. but not obscuring the nail; metatarsus and digits usually darker than the manus but varying from bistre to buffy brown and paling proximally to buff; the margins may be either lighter or darker than the dorsum.

The fur of the tail base shares the body colour and length for 30 mm. or so, but is then shortened to 15 mm. and its colour enriched to a red brown (russet to tawny) which may extend over half or more of the dorsal and lateral surface. The fur is then progressively lengthened, darkened, and erected, forming a black or brown-black dorsal crest reaching 30 mm. at the apex. The lateral surfaces are coloured like the dorsum and may or may not contribute to the brush. The ventral surface in adults is always much lighter (cinnamon buff to cream buff) and the hair is bristly and adpressed distally, where scale exposure by abrasion may occur. The hairing and colour of the tail varies considerably, chiefly with age; the blackest and most extensive crests are in subadults, and in such there may be a coextensive blackening of the ventral surface, but never a ventral duplication of the crest.

The chief variations of pelage, which are of a marked kind, are clearly age characters and independent of sex and season. In subadults as late as the P³M³ stage, which may be almost full grown, the

coat is softer and looser in texture, and the overlay of guard hairs and the resulting grizzling much reduced. The subterminal band of the underfur pales to olive buff or buffy brown and of the guard hairs, to ivory or near white and the pale basal grey shows through to the surface—the resulting dorsal colour being a weak grey brown or drab. A fully furred pouch young (head and body ea. 210 mm.) shows a smooth adpressed coat about 13 mm. long dorsally, with a colour scheme similar to the adults, but even darker and richer.

The adult pelage of this Western Australian series as given above is notably different from other bettongs I have examined—darker, browner, and with less contrast between the subterminal band and the external colour. The darkest examples are quite close to the pelage of *Potorous tridactylus*. In subadults the difference is less and skins of all species which have been immersed for long periods in saline preservatives may justify Thomas' phrase "not definitely different."

The hair tracts in the above pouch young are in substantial agreement with Boardman's figures (1943, fig. 17 and 18) except in the vicinity of the eye. Here a strongly conspicillate effect is produced by radial tracts from its margins interrupting the general caudad flow on the face; that from the anterior canthus is a direct reversal of considerable extent and is marked off by strongly developed opposition ridges. On the tail, the distal flow of the lateral surfaces has an upward inflection, and the mid dorsal tract which is strictly distal, is separated from it by converging ridges; a similar condition occurs in *Caloprymnus* at the same stage. In adults the condition in *penicillata* is much as in *lesueuri*.

CRANIAL CHARACTERS (Pl. xxix, fig. A-F): The treatment of cranial and dental characters is made to cover some areas of conflict in existing accounts and to supplement these where possible and is chiefly based on a series of 14 skulls, drawn in equal proportion from south-west Western Australia and from lower South Australia. A preliminary comparison (infra) having shown it to be sufficiently homogeneous for treatment at subspecies level, I regard it as representing *B. penicillata ogilbyi* Gould, and use it as a standard for the definition of other forms. The comparisons made are with *B. lesueuri* unless otherwise stated, and where metrical, with the means of the three populations of that species studied (supra). Individual variation both metrical and nonmetrical is considerable, but much less than in *B. lesueuri*; the mean variation for 24 cranial measurements being 10 per cent.

In general form the skull is close to that of *B. cuniculus*. When fully adult it is longer than in *B. lesueuri* but narrower and shallower, so that the overall size as measured by the displacement volume (54 cc.) is scarcely greater than in Central Australian *B. lesueuri*. The ossification is lighter, and the surfaces smooth, with muscular impressions reduced; mean adult weight 16 g.

The chief regional difference is in the rostrum which is longer, yielding a rostral index of 43 and facial index of 226 as against 36 and 178 respectively; it is also relatively wide and deep basally and forms a steeply tapering cone without the lateral constriction or dorsal flattening of *B. lesueuri*. The nasal bones are both actually and relative to skull length, longer and narrower posteriorly, but their shape varies, partly at least as an age character. In subadults the posterior margins are often sinuous and irregular and invaded by spurs from the frontals and the lateral are suddenly constricted at the maxillo-premaxillary suture, giving shapes like some of the *B. lesueuri* variants. In adult and aged skulls the posterior margins are transverse and nearly rectilinear and are well in advance of the interorbital line; the junction is sharply angular with the lateral margin which converges evenly to the anterior nares, where it is suddenly constricted to a sharp apex, over-reaching the gnathion anteriorly—a condition different from any phase of *B. lesueuri*. The zygomatic arches are shorter as well as narrower, with the maximum width posterior to mid point, rarely anterior to it; the interorbital space wider, less concave and virtually unconstricted throughout life, an incipient post-orbital process impressed on their edges, and the temporal ridges scarcely evident before the tooth change, and always weak. The interparietal is variable, similar to *B. lesueuri* when present, but sometimes not developed or very early fusing with the parietals.

In lateral aspect, the premaxillae make a larger contribution to the wall of the rostrum, their nasal suture equal to or greater than, the maxillary; malar much weaker, its median depth but half that of *B. lesueuri*; the supratympanic canal is not completed by bone and the squamosal-frontal contact at the pterion, is invariable.

The palate is longer and wider than in *B. lesueuri* and differently shaped owing to the extraversion of the secutor and anterior divergence of tooth rows. The anterior palatal foramina are variable, with dimensions overlapping those of *B. lesueuri*, but yielding means above the Central Australian and about equal to the lower South Australian population of that species. The posterior vacuities vary both

in size and site, but in general are smaller and usually lie entirely within the palatine bone, whereas in *B. lesueuri* they are bounded anteriorly by the maxilla. The diastema is the longest in the genus, averaging 20 per cent of the basal length. The alisphenoid bulla is much smaller, its chief diameter relative to basal length being 25% lower; it is still, however, a prominent feature, quite similar in general shape, and in size, the second in the subfamily; it is not transparent as stated by Thomas, unless very greasy.

The mandible is slighter throughout, with most dimensions 10-15% below the *B. lesueuri* means, the diastema alone being longer. The lower border is less convex, the ascending process less erect, and the masseteric foramen, though variable, usually decidedly smaller.

Sexual differentiation cannot be adequately assessed, but is apparently slight, the female as large as the male. Age changes slight but more definite than in *B. lesueuri* and chiefly shown by the shorter rostrum and relatively wider nasals in the subadult skull and a lag in the expansion of the bulla and mandibular condyle.

DIMENSIONS: The following figures give the range and mean of skull dimensions in mm. for (1) 5 adults at P¹M¹, of both sexes; and (2) 5 subadults at P³M³ of both sexes: greatest length, 76.8-81.0 (78.3), 70.5-74.5 (72.4); basal length, 64.5-68.5 (66.1), 59.8-62.8 (61.1); zygomatic breadth, 39.6-42.7 (41.4), 38.7-40.1 (39.4); nasals length, 31.0-32.6 (31.8), 27.5-30.5 (28.9); nasals, greatest breadth, 12.0-14.3 (13.3), 13.0-13.7 (13.4); nasals, least breadth, 6.3-7.9 (7.3), 6.2-6.8 (6.5); rostrum depth, 14.3-15.9 (14.9), 12.6-15.0 (14.0); interorbital constriction, 16.8-18.4 (17.7), 16.3-18.0 (17.3); palate length, 42.0-45.4 (43.8), 38.5-41.4 (39.8); palate breadth inside M², 12.0-13.2 (12.4), 10.8-12.4 (11.8); ant. palatal foramina, 2.9-4.0 (3.4), 2.5-3.2 (2.9); diastema, 12.7-14.0 (13.5), 12.0-13.7 (12.7); bulla length, 13.8-15.0 (14.4), 12.8-14.2 (13.3); bulla breadth, 9.6-10.1 (9.9), 8.2-9.1 (8.5); basiscranial axis, 19.2-22.3 (20.5), 18.3-20.0 (19.0); basifacial axis, 45.2-47.5 (46.2), 41.1-43.6 (42.5); facial index, 213-236 (226), 210-237 (224); mandible, maximum breadth, 38.5-43.0 (40.3), 35.9-39.1 (37.8); depth of ramus below M², 8.9-9.8 (9.2), 8.0-9.0 (8.4); breadth ascending process, 11.6-13.6 (12.7), 10.2-12.0 (11.3).

The series contains larger examples than have hitherto been recorded.

DENTITION (Pl. xxx, fig. A-J and O): The dentition is similar to that of *B. lesueuri* but less specialized and with a greater residuum of phalangeroid characters; it was regarded by Bensley as directly

linking the genus with *Hypsiprymnodon*. In most categories the dimensions overlap those of the Central Australian series of *B. lesueuri*, but are decidedly below the means of the three populations of that species reviewed above, and there is a general tendency to narrowness and slightness, though there are one or two exceptions to that. The mean variation in dimensions of functionally stable teeth is slightly lower (14%). In the following account the comparison throughout is with *B. lesueuri* unless otherwise stated.

The incisor rows meet at a narrower angle and are more separate from the canine. I^1 is a smaller tooth, rather less upright, and with its labial face lateral throughout life. Dorso ventral height 5.5-6.4 (5.8); anteroposterior length 2.2-2.5 (2.3). I^2 much narrower and with its anteroposterior length about equal to that of I^3 , not notably longer as might be inferred from Bensley's comparison with *Hypsiprymnodon*; it is the first of the prediastemal series to erupt; anteroposterior length 2.3-3.0 (2.5); transverse breadth 1.6-1.9 (1.8). I^3 with its crest more normally aligned in the incisor row; its shape much as in *B. lesueuri* and with similar changes with wear; dorso ventral height 2.8-3.7 (3.2); anteroposterior length 1.9-3.0 (2.4). The labial face of all three incisors is longitudinally grooved more frequently than in *B. lesueuri*, but there is much variation—fig. A shows a strongly grooved phase of I^1 and I^3 . I , longer and more slender, with a greater tendency to slight upward curvature weakly suggestive of *Petaurus* and *Distoechurus* in the Phalangeridae; anteroposterior length 11.4-14.5 (12.7); breadth 3.0-3.3 (3.1).

The canine is a larger tooth, showing similar variation in shape; dorsoventral height 4.5-4.8 (4.7).

Dental differences between *B. lesueuri* and *B. penicillata* culminate in the permanent premolars, the two species representing in this feature the extremes of specialization and conservatism, within the genus. The chief distinctions of P^4 in the latter are its smaller size, hypsodontism, and extraversion of its axis, and convexity of crest anteriorly.

In the present series, while the angle of rotation is fairly constant, the degree to which the posterior portion of the blade abstains, varies. The body of the tooth, however, is always decidedly curved, its outlines as seen from above following a shallow sigmoid, with a constriction at the posterior one-fifth and maximum breadth at the anterior one-third of its length. A posterointernal talon is always developed, but is quickly reduced by wear; an internal ledge scarcely

differentiated. In profile the unworn crest undulates; an anterior rounded and grooved portion, and a smooth posterior cusp, being separated by a shallow declivity, but equality of height is soon attained by wear. In contrast, the enamel wall of the crown is nearly twice as high anteriorly as posteriorly; its grooves are constantly seven on the buccal wall and are either vertical or converge to the centre of the crest; they are generally wider than in *B. lesueuri*. In unworn or slightly worn examples, anteroposterior length 7.0-7.4 (7.1); breadth 2.8-3.2 (3.0); height (of enamel) 4.3-4.6 (4.4).

The lower secator P_1 is simpler than its opponent, 10% shorter but with breadth and height slightly greater, relatively; extraversion of its axis is even throughout its length; its outline from above almost straight sided, with the greatest breadth near the anterior one-third; no talon is developed. The profile of the crest is quite straight and the enamel of the wall higher anteriorly; grooves constantly seven; anteroposterior length 6.2-6.7 (6.4); breadth 2.7-3.0 (2.9); height (of enamel) 4.1-4.3 (4.2).

P^3 is very much smaller than the secator, but generally similar to the anterior half of that tooth; evenly rotated outwards and with its maximum breadth median and its outline from above oval except for a re-entrance at the posterointernal corner; the profile of its crest straight or at most very slightly rounded; its enamel wall as in the secator; grooves constantly five. In the skull of a pouch young, the crest of P^3 which is erupting, shows no extraversion, but lies parallel to the midline of the palate; anteroposterior length 4.0-4.6 (4.4); breadth 2.4-2.7 (2.6); height of enamel 3.5-4.3 (4.0). P_2 similar to its opponent, scarcely reduced, but more evenly oval; grooves five; anteroposterior length 3.7-4.1 (4.0); breadth 2.5-2.7 (2.5); height of enamel 3.5-4.4 (3.9).

The upper deciduous premolar MP^1 is similar to that of *B. lesueuri*, but smaller; markedly smaller than M^3 ; the blade of the anteroexternal cusp is less developed and its crest more oblique to that of P^3 . It is the first of the cheek teeth to erupt, its appearance synchronising with I^2 and preceding P^3 . Its lower opponent MP_1 is also smaller, but with its anterior lobe relatively wider than in *B. lesueuri*; the crest of the anterointernal cusp is obscurely notched on its outer surface, and meets that of P_2 more directly than in the upper tooth. Dimensions of seven examples of MP^1 and MP_1 respectively, showing slight to moderate wear are: anteroposterior length 3.0-3.6

(3.3); 2.8-3.5 (3.0); breadth anterior lobe 2.6-2.8 (2.7); 2.0-2.5 (2.3); breadth posterior lobe 3.0-3.3 (3.1); 2.4-2.7 (2.5).

The molar rows, which in relation to skull length are the shortest in the genus, diverge anteriorly in straight lines. The *absolute* size range of all molars as shown by the crown areas overlap the minimum for the combined *B. lesueuri* groups, but the means are decidedly lower (from 4 to 19%), the inferiority being greater in the second and third of both upper and lower series.

The interrelations of crown areas are generally similar to those of *B. lesueuri*, but there is an increase in the *relative* size of the first molars, both upper and lower, and a decrease in the second and third. In the upper jaw this creates a tendency towards subequality of M^1 and M^2 and in the lower jaw to dominance of M_1 over M_3 , both conditions being rare or of minor frequency in *B. lesueuri* and quite absent in *B. cuniculus* where the latter condition is excluded by a characteristic enlargement of M_3 . The index of reduction or ratio of largest to smallest molar, is lower (less steep) than in *B. lesueuri*, the mean values for the upper and lower series respectively being 2.9 and 2.0 as against 3.3 and 2.3 in the latter. The molar formulae and their approximate frequencies and the percentage relation of the crown areas of individual teeth to the corresponding first molars, is as follows: in the upper jaw $M^2 > M^1 > M^3 > M^4$ 50% $M^1 > M^2$ 42% $M^1 = M^2$ 8%; M^3 and M^4 being constant in the sequence; and M^1 100; M^2 90-107 (99); M^3 70-80 (75); M^4 26-43 (36). In the lower jaw $M_2 > M_1 > M_3 > M_4$ 83%; $M_1 = M_3$ 8%; $M_3 > M_1$ 9%; M_2 and M_4 being constant; and M_1 100; M_2 107-120 (113); M_3 90-103 (96); M_4 48-70 (56).

The size and shape relationships of the corresponding upper and lower molars and their variations, and the relation of anterior to posterior lobe, are much as in *B. lesueuri*; the breadth/length ratio tends to be slightly lower than the *B. lesueuri* means in the upper teeth, and slightly higher in the mandibular set.

The range and mean of the anteroposterior length, breadth anterior lobe, and breadth posterior lobe in the molars of the bisexual series of eleven skulls is as follows:— M^1 3.7-4.2 (4.0); 3.5-4.4 (3.9); 3.7-4.3 (4.0). M^2 3.6-4.5 (4.0); 3.8-4.4 (4.0); 3.5-4.2 (3.8). M^3 3.5-4.0 (3.7); 3.2-3.8 (3.6); 2.7-3.2 (3.0). M^4 2.2-3.0 (2.5); 2.0-2.9 (2.5); 1.7-2.3 (1.9). M_s^{1-3} length in situ. 11.0-12.7 (11.8). M_1 3.5-4.0 (3.7); 3.2-3.7 (3.5); 3.5-4.1 (3.6). M_2 3.8-4.2 (4.0); 3.7-4.1 (3.9); 3.6-4.0 (3.8). M_3 3.5-3.9 (3.7); 3.5-4.0 (3.7); 3.2-3.7 (3.4). M_4 2.7-3.5 (3.0);

2.7-3.2 (3.0); 2.7-3.2 (3.0); 2.1-2.7 (2.3). Ms_{1-3} length in situ, 11.1-12.5 (11.5).

The crown pattern of the molars is very similar to that of *B. lesueuri*, but with the cusps and lophs lower and less prominent. An accessory cuspule originating at cingulum level on the buccal wall of M^1 and M^2 and sealing that aspect of the median valley, is developed in about half the series, and more rarely appears on MP^4 and M^3 ; the analogous feature on the lower molars, mentioned by Bensley, has not been traced. M_4^1 are somewhat less variable than in *B. lesueuri* and simulate more or less crudely the main structural features of M_3^2 .

The series affords no example of the tooth change, but the eruption of P_4^1 may be delayed beyond that of M_4^1 ; this, however, is as likely to be due to precocity of M_4^1 as to retarded secators, as it occurs in skulls still metrically and suturally subadult. There is no instance in this series of the secator preceding the 4th molar as is frequent in *B. lesueuri* and *B. cuniculus*, so that, on the whole, a later tooth change seems indicated for *B. penicillata*.

SUBSPECIFIC DIFFERENTIATION IN *Betlongia penicillata*.

B. penicillata ogilbyi, Gould: The western representative of *B. penicillata* in the Swan River districts was early separated by Gould and Waterhouse (1841) from the type of New South Wales, as a full species under the name *B. ogilbyi*; while a single immature skin from South Australia, was made the type of a third species, *B. gouldi*, by Gray in 1843. Later examination of more material from all three localities revealed much local variation and overlapping, and Thomas in 1888 merged both names in *B. penicillata* Gray 1837, and it is only in recent years that they have reappeared in subspecific form, without, so far as I can ascertain, any new evidence in support of this course, being adduced.

I have examined no material certainly localized in New South Wales, but the local variation in south-west Western Australia outlined above is sufficiently wide to vitiate most of the pelage distinctions claimed for the eastern animal and the metrical differences implied by Waterhouse's and Gould's data, are not significant when compared with the range in the present series except possibly for the secator, which is confirmed by Tate for North Queensland (1948 *op. cit.*, 267). The eastern animal would appear to be very weakly differentiated, with at most a slightly greyer pelage, occasionally longer secator, and possibly some slight differences in nidification.

The South Australian animal, so far as it can be understood from material available here, is even less distinct from the western one. In the South Australian Museum are two skins and six skulls which although without reliable data, are probably of local origin; two of the skulls almost certainly so. A close and detailed comparison of the cranial and dental characters of these skulls with Western Australian material from the south-western districts only, discloses slight average differences of which the following are the chief. (1) The rostrum tends to be slighter in the South Australian skull. (2) The zygomatic process of the squamosal is also slighter, more concave above and the adjoining squamosal more inflated. (3) In the mandible the mandibular foramen is often larger. (4) The antemolar teeth are virtually identical, but in the molars the condition $M^1 > M^2$ is twice as frequent in the South as in the Western Australian group. The variation in all characters is high and this with the inadequacy of the samples, casts doubt on the significance of the differences, which in any case are somewhat less than those separating the Central and South Australian populations of *B. lesueuri*. The overall similarity of the two samples from localities so remote is much more impressive. The two South Australian skins present no characters which cannot be reconciled with the Western Australian range.

These findings appear to me to justify and confirm the clear statements of Gould and Waterhouse (*op. cit.*), often overlooked, that "*B. ogilbyi*" of the Swan River districts, also occurred with very slight modification in the State of South Australia, and if Krefft (1864) is right, extended far beyond it, into the lower Darling Basin of New South Wales.

The Waldana karpitchi: This was taken about 1897 by R. T. Maurice at Waldana Spring on one of the preliminary journeys which culminated in his traverse with Murray from Fowler's Bay to the Cambridge Gulf, in 1902. The locality is about 125 miles north-west of Ooldea in the arid western division of South Australia, and about 100 miles south of Pundi, whence came the most southerly of the reports I had of it from the Pitjanjarra in 1934. Maurice mentions having seen "kangaroo rats" in some plenty both south and north of Waldana, but what species are involved in this observation is doubtful.

The specimen (South Australian Museum, registered number M.4140) is an alcohol preserved female pouch young having the dimensions: head and body, 173; tail, 190; pes, 78; ear, 28. The pelage in its present condition is paler and more grizzled than is usual in *B. penicillata ogilbyi*, but it is a moot point how much of this is

due to bleaching during the 60 years of its partial immersion in spirit. The colour distribution on manus, pes and tail is quite as in *ogilbyi*; the tail darkening rapidly distally and forming a low but distinct black brush over the terminal third. The skull (greatest length 46.6 mm.) is functionally edentulous or nearly so, but I^1 and I^2 and the third and milk premolars of both jaws are sufficiently advanced for examination of their crowns after removal of soft tissue.

This is the only fleshed specimen of *B. penicillata* from an eremian district which I have examined and it is unfortunate that its immaturity and storage history render a full appraisal, at subspecies level, impracticable. In essentials it is reconcilable with the standard *ogilbyi* series reviewed and is quite distinct cranially from the form *anhydra* from 470 miles further north.

No skull of *B. penicillata ogilbyi*, strictly matched dentally with the Waldana specimen, has been available for comparison, and growth changes in the skull are so rapid at this stage, that differences between individuals are of doubtful significance. Nevertheless it seems questionable to me whether the Waldana skull at dental maturity would have attained to either the maximum length or relative rostral development of full scale *ogilbyi* and the length of MP^4 , which is the most advanced of the teeth and appears to be fully formed, is below the mean of the standard series (2.9 cf. 3.3 mm.). If these three differences were realized in the adult it would suggest affinity with the small skulls next considered, with taxonomic implications which are there indicated.

"*B. penicillata gouldi*" Gray: The type of Gray's *Bettongia gouldi* was a small skin without skull believed to be immature, but the second specimen reviewed by Waterhouse (1846, 22, Pl. 6, fig. 1) in the same connection was an adult skull of very small size. The present material includes a very similar skull, which, though not formally localized, may be inferred from associated material and other evidence to be from the western slopes of Mount Lofty; this has been closely compared with the standard *B. penicillata ogilbyi* series with the following results.

It is an advanced subadult at P^3M^3 , and remarkably small in the relevant age group of *ogilbyi*; 18 of 23 linear dimensions studied falling below the range of these, with an average difference from the mean of -13%; its displacement volume is only 60% of that of *B.p. ogilbyi*. Differences in proportional development (shown by the percentage relationships of dimensions to the basal length) exceed

5% in 10 items; the chief changes being in anterior palatal foramina, length of bulla, breadth and depth of mandible (+8 to 12%) and palatal breadth and facial index (-12 and -11% respectively). Laterality in the posterior structures of the mandible is especially noticeable, the transverse breadth of condyle being +14%; the mandibular foramen of the same region, is both actually and relatively the widest in the series; otherwise nonmetrical differences are absent and the general appearance of the skull normal for *ogilbyi*.

The dentition as a whole is proportionately reduced, with, however, a slightly narrower I^3 and slightly stouter P_3^3 . The crown area sequences and percentage ratios are: M^2 103 > M^1 100 > M^3 73 and M_2 113 > M_1 100 = M_3 100 and the index of reduction (three teeth only) is 1.4 (upper) and 1.1 (lower); these size relations can all be closely matched in the standard series of *ogilbyi*.

The dimensions of this skull are:—greatest length 62.5; basal length 52.5; zygomatic breadth 36.0; nasals length 23.5; nasals greatest breadth 10.5; nasals least breadth 5.8; rostrum depth 12.0; interorbital constriction 14.5; palate length 32.8; palate breadth inside M^2 9.0; anterior palatal foramina 2.8; diastema 10.8; bulla 12.4 x 7.3; basiscranial axis 17.5; basifacial axis 35.0; facial index 200; mandible: maximum breadth 36.2; depth below M_2 8.2; breadth ascending process 10.6; breadth of condyle 4.8. Ms_{1-3} 9.7. Ms_{4-5} 9.6. P^3 and P_3 respectively: length 3.5; 3.3 breadth 2.5; 2.5 grooves 5; 5. The agreement with the older skull of Waterhouse, so far as it can be studied from his account, is very close. The palatal length given by Waterhouse (11 lines) is evidently a typographical error.

The general level of differentiation reached by these small skulls is quite appreciable and is distinctly greater for example than that shown by the South as compared with the Western Australian moieties of the *ogilbyi* series used as a standard. But though they are by no means mere miniatures of the *B. p. ogilbyi* skull, their taxonomic recognition raises biological objections and seems to me contraindicated. On the one hand, to treat them as representing a subspecies of *B. penicillata*, existing in very small numbers side by side with *B. p. ogilbyi* at widely separated points, is to violate the chief principle held to underlie the equilibrium between geographic races, by attributing to it a reproductive isolation which should not exist at subspecific level. On the other hand to treat them as representing a full species is clearly unjustifiable on morphological grounds.

The alternative is to regard them, as Waterhouse suggested, as dwarfed examples of *ogilbyi* owing their distinctions to individual and physiological rather than genetic causes. This is supported by the existence in the same region of similar though less marked dwarfism in the allied species *lesueuri*, where subspecific distinction could not be seriously considered. Dwarfism and gigantism within species of Australian mammals, especially under eremian conditions, offers an interesting field for the study of changes in proportional development with changing body size. The amplitude of the size difference in material otherwise strictly homogeneous at subspecies level, is often astonishing, as shown for example by Spencer (1896, 25) and Wood Jones (1923a, 106) for *Dasymercus* and which I have confirmed in the subspecies *hillieri* of the Lake Eyre Basin (1933), and in *Rattus villosissimus*.

"*B. gouldi*" as a form (either specific or subspecific) occurring between the head of Gulf St. Vincent and Mount Lofty in territory densely occupied by *B. p. ogilbyi*, under a 20-30 inch rainfall, is difficult to accept. But the case might be different if these localities were erroneous and the material were derived from further north. It might well then represent a subspecific eremian offshoot of *ogilbyi*, to which the Waldana specimen from 600 miles north-west of the head of the Gulf, should be referred.

In the absence of this evidence, I am confirmed in the rejection of these dwarf skulls from lower South Australia as representing a distinct race or species (whether "*B. gouldi*" or not) by the existence of two others in which the distinction of even smaller size, is reinforced by structural changes of a much more decided kind, and by adequate geographical isolation.

Bettongia penicillata francisca Finlayson, 1957: This form was based upon a portion of a skull in the old collections of the South Australian Museum (Registered number M. 5484), which came from St. Francis Island, Nuyt's Archipelago, off the Eyre Peninsula coast of South Australia in approximately 32° 35' S. lat. and 133° 20' E. longt.; no other details of its provenance are recorded.

The specimen lacks the occiput, nasals and mandible, but has a complete adult maxillary dentition, together with the two first incisors and I² of the right side. The dimensions available suggest a complete skull of about the same size as the Mount Lofty dwarf in its present subadult condition. As compared with *B. penicillata ogilbyi*

of the adjacent mainland, the rostrum, while normal in shape, is probably reduced in relative length though the rostral index cannot be determined. The interorbital breadth and breadth of palate are relatively greater, and the anterior palatal foramina longer.

The incisors are worn and damaged and little of differential value can be inferred from them, but the premolars and molars are well preserved, though the crowns of the latter show heavy wear. The secator, P⁴ (Pl. xxx, fig. M and N) conforms in a general way to that of *penicillata s. lat.* in its long axis being rotated outwards from the midline of the palate; in the wall of the crown, being twice as high anteriorly as posteriorly; and in the broad grooves. It differs from *B. p. ogilbyi* in the extraversion of the axis being less in degree and more even in mode, with less torsion of the crest; in reduction of the grooves from seven to six and in its greater breadth. The last distinction is critical; while the length of the tooth is reduced by nearly 20% as compared with the means for *ogilbyi* its breadth is actually increased by 6%, leading to a breadth/length ratio of .55 as against .42. The general appearance of the secator is similar to P³ of *ogilbyi*, but it differs in its distinct posterointernal talon and much greater bulk, which is 2½ times that of P³ in the Mount Lofty dwarf of the same cranial size.

The crown areas of all the molars (Pl. xxx, fig. N) are below the range for *ogilbyi*; the reduction being much less on M¹ and M² than on M³ and M⁴. The percentage size ratios calculated from the crown areas are: M² 105>M¹ 100>M³ 68>M⁴ 24, yielding an index of reduction of 4.4 as against a maximum of 3.8 in *ogilbyi*.

DIMENSIONS: interorbital breadth, 15.0; palatal length, 34.5; palatal breadth inside M², 11.2; anterior palatal foramen, 3.2; Ms.^{1,3}, 10.4; P¹ length, 5.8; P⁴ breadth, 3.2.

The former presence of this bettong on St. Francis Island was recorded by Wood Jones (1923b), who inferred from the descriptions of those who had known it in life, that it represented *penicillata*. The external characters are otherwise unknown, and the present fragment, as far as I am aware, is the only material relic of the animal, which is believed to have become extinct some 70 years ago.

Bettongia penicillata anhydra Finlayson 1957: The type and only known specimen of this form, is a part skull with mandible (South Australian Museum, registered number M. 3582) from an animal in the flesh collected by M. Terry in July 1933 near the McEwin Hills

of the Lake Mackay area of Central Australia, in approximately $22^{\circ} 2'$ S. lat. and $129^{\circ} 47'$ E. longt. The external characters are not known with sufficient precision for recording.

The skull (Pl. xxix, fig. G and H) lacks the occiput, basioccipital and posterior portion of the bullae but has a complete mandible. Suturally and dentally it is fully adult but not aged, and the dentition which is complete, shows moderate wear. In general size it is inferior to *francisca* and is the smallest skull of the genus yet examined; its estimated displacement volume being 34 cc. approx. as against a mean value of 54 cc. in the standard series of *B. penicillata ogilbyi* and 53 cc. for the Central Australian *B. lesueuri*. In absolute dimensions, 17 of the 19 items tested fall below the minimum for *ogilbyi* with an average difference from the means of 20%. Proportional development as determined by the percentage relation of dimensions to the length, disclose a high order of distinction from *ogilbyi*, the mean difference in this category being 11%. The chief proportional changes are: zygomatic breadth + 13%; interorbital constriction - 13%; diastema - 24%; breadth of bulla + 25%; depth of mandibular ramus + 17%; breadth of ascending process + 26%. In addition the rostrum is much shortened, the rostral index falling to 34 as against 43 in *ogilbyi*.

Some of these changes indicate convergence towards *B. lesueuri*, but especially characteristic are the following: the narrowness and general weakness of the muzzle region; the narrowness of the nasals; the very short anterior palatal foramina and a strongly developed interorbital constriction, unique in the genus. The braincase is relative narrow and more tapered anteriorly than in either *B. lesueuri* of Central Australia or *B. penicillata ogilbyi* and the temporal crests, which are strongly developed, are differently disposed towards the midline. In the mandible, the proportions of coronoid, ascending process and mandibular foramen are nearer *B. lesueuri*, and the relative depth of the body of the ramus is actually greater than in that form.

In the dentition, the incisors show characters of both species, I^2 being broader than is usual in *B. penicillata ogilbyi* and I^3 lacking the inturning of the crest, seen in *B. lesueuri*. The secator, P^4 (Pl. xxx, fig. L and K) is actually longer and as broad as in the much larger *ogilbyi* skull, but its height is about 10% less and is more evenly distributed along its length. It shows many of the fundamental characters of the *B. penicillata* secator and in extraversion of its axis and torsion of crest is intermediate between *B. p. ogilbyi* and *B. p.*

francisca; its grooves are wide and seven or eight in number. Morphologically the tooth differs widely from its *B. lesueuri* analogue, in its relatively greater breadth; greater anterior height yielding a height/length ratio of .47 as against a mean of .42 in Central Australian *B. lesueuri*; and in the extraversion and torsion of its crest, which are not remotely approached by any specimen of *B. lesueuri* in the three populations studied, in which a straight crest and distinct introversion are invariable. The outturning of the lower tooth P_4 is less marked; its crest is straight and its grooves are reduced to seven.

The length of the molar rows *in situ*, and the crown areas of all the molars individually, are below the minima for *B. penicillata ogilbyi*. The reduction, as in *B. p. francisca*, is least on the first and second molars, and greatest on the third and fourth, but the colateral disparity between these pairs is even greater, and the fourth molars are extremely small teeth. M^1 on the other hand is particularly large and broad as in *ogilbyi*. These changes lead to an unprecedentedly high index of reduction (greatest crown area/least) in both upper and lower jaw as follows: *B. p. anhydra* 6.5 upper, 4.2 lower; ⁽¹⁾ Central Australian *B. lesueuri*, 1.9-5.1 (3.3), 1.5-3.2 (2.3); and *B. p. ogilbyi*, 2.4-3.8 (2.9), 1.7-2.3 (2.0). The size sequence of the molars and the approximate percentage relation to the first molar, as gauged by the crown areas, are: M^1 100 > M^2 94 > M^3 62 > M^4 15 and M_2 108 > M_1 100 > M_3 81 > M_4 26; these sequences occur in both *B. penicillata* and *B. lesueuri*, but are more frequent in the former. The upper molar rows are slightly curved and there are no supernumerary cusps on the anterior members. Dimensions: greatest length, 62.1; zygomatic breadth, 37.4; nasals, length, 23.7; nasals, greatest breadth, 9.5; depth of rostrum, 11.6; interorbital constriction, 12.2; palate length, 32.5; palate, breadth inside M^2 , 9.4; anterior palatal foramina, 2.4; diastema, 8.0; bulla, anterior breadth, 10.4; mandible, depth below M_2 , 8.7; breadth of ascending process, 13.3; P^4 and P_4 respectively, length 7.5, 6.4, breadth 3.0, 2.8; Ms_{1-3} , 10.5; Ms_{1-4} , 10.2; I^1 dorsoventral height 5.3; anteroposterior length 2.1; I^2 anteroposterior length, 2.5; transverse breadth, 1.8; I^3 dorsoventral height, 2.6; anteroposterior length, 2.2.

As stated in the original description, this skull presents a blend of the characters of *B. lesueuri* and *B. penicillata*, with a basis of intrinsic features. The combination, if constant, would undoubtedly merit recognition at full species level, but in the absence of any

(1) Wrongly cited in the original description as 3.9.

further material to supplement the holotype, I find the possibility of metrical anomalies introduced by dwarfing, and the lack of any information on the external characters of the animal, a sufficient deterrent to that course. While the balance of likeness is perhaps towards *B. lesueuri*, the highly diagnostic P⁴ is so different from the secator of that species, and has so much in common with that of *B. penicillata*, that I have chosen to associate it provisionally with the latter as a subspecies.

The overall development of the *Bettongia penicillata* group though very imperfectly known, would seem to be served by the conception of *B. penicillata ogilbyi* as a dominant south-western race extending east from the Swan River districts by way of coast lands into South Australia and beyond into the eastern portions of the Darling basin of New South Wales. *B. penicillata penicillata* would then represent a poorly differentiated highland race distributed on a north-south axis chiefly on the western slopes of the Great Divide, and possibly extending into a subtropical littoral zone round the Gulf of Carpentaria both in Queensland and the Northern Territory. *B. gouldi* Gray as at present known is void and founded on local dwarfs of the *ogilbyi* populations, while *anhydra* and *francisca* may have arisen from similar dwarfs, stabilized and further differentiated under eremian and insular conditions respectively.

STATUS OF OTHER MEMBERS OF THE SUBFAMILY IN THE REGION.

Several aboriginal vocabularies contain words for animals which, while but vaguely known to the present generation, are suggestive of members of the present group, either from the general drift of the account or from the voluntary selection of known members of it, for comparison. One such is the *tehunaki*, of the Pitjanjarra and Yankunjarra, which, though known to many of the older people, has not been seen nor taken for many years in the granite ranges about the 26th parallel, which was its locus. It is compared always, though in varying terms, to the *karpitchi* or the *tehungoo*. These last, representing *Bettongia penicillata* and *B. lesueuri* respectively, together with *Caloprymnus campestris* Gould of the Lake Eyre Basin are the only species of which there is definite evidence as living or recently living forms in the Centre and adjacent arid tracts.

Since I recorded the sudden increase of *Caloprymnus* in the Lake Eyre Basin (1932; 1936.) there have been few, if any, reliable reports of it. Bolliger (1938) published some observations on a rat kangaroo to which he gave this name, but he has since been good enough to inform me (in litt) that the identity was mistaken and that the animal (an unlocalized zoological gardens exhibit) was probably *Aepyprymnus rufescens*. All attempts to trace *Caloprymnus* as a living or recently extinct species beyond the limits mapped in 1932 have given only negative results, but the finding of skeletal remains in caves of the Eucla district (Lundelius 1957) tends to confirm Tate's statement (1879) of its presence at the head of the Great Australian Bight eighty years ago. This I was inclined to reject in 1932 as no material of the species is mentioned by Tate, while on the other hand, skulls in the old collection of the South Australian Museum, which had been labelled *Caloprymnus* (possibly by Tate), were actually *B. lesueuri*.

Potorous, as a genus of modern species, seems to be almost entirely subcoastal in its mainland distribution. Early compilers of faunal lists claim more than one species for lower South Australia, and there is a rural tradition that *tridactylus* occurred in the lower South-East District of the State, but Thomas's (1888, 120) record of a skull from the Murray River is the only material evidence in support. The extent of its inland diffusion is quite conjectural, but from what is known of the habitat preferences of the species, it is very unlikely that it occupied the subarid districts in modern times. Zietz's use (in Gill 1909) of *Potorous tridactylus* for an animal at Port Lincoln is probably based on *Bettongia penicillata*.

Several references to *Bettongia gaimardi* Desmarest exist in early lists of South Australian mammals, which may be derived from the statement of Waterhouse (1846. 207), but no confirmation of this has been obtained in the succeeding years. The forms described here as *B. penicillata anhydra* and *B. penicillata francisca* were closely compared with the standard descriptions of *B. gaimardi* but no evidence of any special affinity to that form could be found.

In the South Australian Museum is a skull of *Aepyprymnus rufescens* Gray of normal characteristics, labelled as from "Lake Eyre." The locality is some hundreds of miles west of the most inland of authentic records of the species and presents features radically different from the known habitats of *Aepyprymnus*. There is no other relevant data, and the anomaly should probably be attributed to a confusion of record.

POST-PLEISTOCENE REPRESENTATIVES OF THE
SUBFAMILY.

The mammal palaeontology of Central Australia except for the Lake Eyre Basin, is almost unknown and the writer has examined no relevant material from these areas. In lower South Australia, however, superficial deposits, ancient camp sites and cave deposits have yielded bones copiously, and the South Australian Museum has considerable collections of subfossils so derived, much of it gathered by N. B. Tindale and his associates in aboriginal archaeology. Small amounts in my own collection have also been available.

The chronology of the collections is in most cases, only vaguely known; the oldest are probably those from layer 11 of the Devon Downs beds which Tindale (1957) links with his Prepirrian culture with a possible age (based on radiocarbon data) of about 5000 B.P. At the other extreme, some of the superficial camp site bones may be coeval or nearly so with the European occupation, though very few specimens of many hundreds examined show signs of gross recency in the form of soft tissue or fat stain.

The Potoroinae in that portion of this material which has been available to me, is referable to known species and the greater part of it to *Bettongia lesueuri* and *B. penicillata*. Of the eleven sites ranging from Hawker in the north to Tantanoola in the extreme south which have yielded *Bettongia* remains, eight contain *lesueuri* and six *penicillata*, while only three contain both. Little or nothing on the former local status and distribution of the species can be deduced from the collection as a whole, however, which consists for the most part of chance surface finds not fully representative of the deposit. In the case of the Tantanoola, Kongarati and Devon Downs finds, where systematic excavation was made, *B. penicillata* was much the more numerous of the two. This accords with the modern status of the two species and probably indicates that it was locally still more dominant at that time, since the densely ossified skull of *lesueuri* is the more resistant to weathering and disintegration; cranial, as distinct from mandibular specimens occur more frequently with *lesueuri* than *penicillata*. Species of *Potorous*, broadly referable to *tridactylus* and *morgani* also occur sparsely. The latter is present for example in level 1 of the Devon Downs deposits of Murundian age and also in the deeper Mudukian beds of level 6. The possible northern extensions of earlier forms of such fossils into the Centre, and especially into the Lake Eyre Basin, derives interest from its bearing on the hypothesis

to which I have referred (1932, 165) of the evolution of *Caloprymnus* there, from a *Potorous* like ancestor, which would be a natural consequence if Spencer's ideas (*op. cit.*) on the evolution of the Diprotodonts, are well founded.

The archaeological site of Tartanga, which is adjacent to that of Devon Downs but considerably older was but sparsely mammaliferous and yielded no Potoroinae. It may be noted here in passing, that the Tartanga *Macropus* molar which was formerly regarded as anomalous with respect to *M. giganteus* and to which Tindale has reverted (1957.9) is probably reconcilable with that species. Examination of larger series than were available at the time has shown that a maximum breadth of 10 mm. in the anterior lobe of M_1 is occasionally reached in the local form, *M. giganteus melanops*. Gould.

A comparison of the cranial and dental features of the *Potoroinae* of these collections, with the series reviewed (*supra*) will be presented elsewhere. Treatment of the skeletal material is deferred pending completion of a review of the general osteology of the group, which is in hand.

REMARKS ON THE DISTRIBUTION AND BIONOMIC INTERRELATIONS OF THE POTEROINAE

In the modern wreck of this remarkable group of mammals the plan of its unfolding into the vast territories, which it formerly occupied, is but dimly to be seen. The contributions of palaeontology are yet to come,⁽²⁾ and the recent distribution, imperfectly known as it is, together with the phylogeny of its members at species level, are the main sources of such insight as may be had, and they leave much unexplained.

Deductions made on a continental scale from what is known of distribution, are apt to be fallacious here, unless due regard is had for the comparatively recent and unequal effects of aridity. This (whether it be a waxing or a waning influence) has undoubtedly left its mark on the range of some species, which were probably first occupied under climates very different from the present. Even such broad questions as the site of origin of the radiation and the directions in which species have diffused are largely speculative. It may

(2) If the molar figured by Johnston (1882) to which attention has recently been redirected by Edmund Gill (1957) is accepted as a member of this group, it would appear to be the earliest recorded occurrence. It came from the beds of One Tree Point, Tasmania, stated to be of Upper Tertiary age.

be noted that there is in a general way a tendency for concentration both of species and population, in the south and east and that Tasmania was occupied by both sections of the subfamily, whereas in the north and west representation is more sparse and neither section attained a footing in New Guinea.

Recent work on the phylogeny of the group by Pearson (1947; 1950), whose main theme in his later papers is the distinction of the rat kangaroos as a whole from the Macropodidae at full family level, has tended to obscure the deep cleavage between the potoroos and bettongs. This was first developed by Bensley (1903) from cranial and dental considerations chiefly and was considered by him to call for subfamily distinction. The merits and demerits of this are variously regarded, but it seems to derive some geographical support from what is known of the present occurrence of the most primitive forms of both sections. Unless the sites now occupied are to be regarded as mere fortuitous residual areas in a much wider former range, they might be accepted as points of origin of two distinct radiations, the one stemming from a *Hypsiprymnodon*-like ancestor in the north-east and yielding the *Bettongia* species and *Aepyprymnus*, and the other arising in the extreme south-west from a primitive *Potorous* species or potoromorph and leading, as Bensley believed, to *P. tridactylus* as its linear end point and to *Caloprymnus* as a highly aberrant offshoot. In both cases the evolution leads from dense scrub or jungle living forms of sedentary habit and restricted range to highly mobile, wide ranging denizens of open forest or plains. The similarity of *Bettongia* and *Caloprymnus* in somatic features is remarkably close but attained through convergence of phylogenetically distinct stocks. Spencer's postulate (1896.L184) of a widely separate origin of *Bettongia* and *Hypsiprymnodon*, the former in the main east-central originating centre of the Diprotodonts and the latter in a north-eastern Torresian site, seems to clash with the generally accepted derivative relation of the two genera.

In the field relations of *Bettongia penicillata* with *B. lesueuri* and *Aepyprymnus rufescens* there is much that is interesting and significant. Morphologically and in relation to the main evolutionary trends of the genus, *B. penicillata* may be regarded as a basal and comparatively generalized form, while *B. lesueuri* and *Aepyprymnus* on the other hand are advanced in the same sense and have in addition adaptive specializations of an individual kind. There is little doubt that over much of South and Western Australia, *B. penicillata* and *B. lesueuri* were truly sympatric, camping and feeding over the same

areas and exploiting ecological combinations of a very similar kind. In the higher rainfall areas *B. penicillata* more than held its own and often maintained much denser populations than *B. lesueuri*. But with increasing aridity this proportion was reversed until in the Centre *B. lesueuri* vastly outnumbered *B. penicillata*, which in all probability was being rapidly eliminated there long before any of the adverse factors of European occupation operated against either species. Here under present day conditions, when population density in relation to total area available is always low, it is doubtful whether direct competition plays much part in the eliminating process, which is probably decided by adaptive deficiencies in the nest-building habit as compared with the fossorial one of *B. lesueuri*. *Caloprymnus*, a nest builder, succeeds in maintaining only a very tenuous hold on the Lake Eyre Basin, where it has no marsupial competitors on the same ecological level.

In eastern Australia, similar relations must have existed between *B. penicillata* and *Aepyprymnus*. Krefft indeed, quoting the blacks, stated that there were considerable discontinuities in the habitats of the two in New South Wales, but in many districts, the Dawson Valley for example, in Queensland, blending of territories or very close interdigitation of the same, must have occurred. The recession of *B. penicillata* from these fertile and well-watered districts, which was also largely independent of European influences, was much more probably due to direct competition, in which *Aepyprymnus*, also a nest builder, would be advantaged by its superior size, and more advanced herbivorous dentition and greater range of food plants.

The general distribution pattern of the species and their contrasting status, suggests that *B. penicillata*, as an earlier protean generalized form gained transcontinental distribution in the absence of competition, and under somewhat more pluvial conditions than now obtain. It was then encroached on by later developing and more specialized forms; *Aepyprymnus* ultimately replacing it in most of the north-eastern coastal areas, *gaimardi* in a portion of the Pacific Slope of the Divide, and *cuniculus* in a later insulated Tasmania; while in the south and west *lesueuri* reached equilibrium with it where the rainfall was assured and supplanted it in the Centre with the aid of increasing aridity. So far as is known, no species of *Bettongia* occurs in the eastern portion of the Lake Eyre Basin which is the present habitat of *Caloprymnus*; the failure of *B. lesueuri* to supplant the indigenous *Caloprymnus* in this area, which is near the eastern frontier of its advance in this latitude, is probably due, like other

similar anomalies in the Centre, to lack of sufficient population pressure in the former to provide the incentive for invasion of a habitat of such rigorous conditions.

SUMMARY

1. The results of field work on Central Australian representatives of the Potoroinae are summarized.

2. The continental distribution and status of *Bettongia lesueuri* Q. and G. and of *Bettongia penicillata* Gray is discussed and the distribution approximately mapped.

3. Detailed reviews of external, cranial and dental characters of authentically localized populations of these species are made and subspecific differentiation assessed in general terms.

4. There is brief treatment of habits, bionomic interrelations, post-Pleistocene representation and related topics.

EXPLANATION OF PLATES

(The dental elements figured are of the right side of the dorsal aspect of the skull unless otherwise stated.)

PLATE XXVII

The skull in *Bettongia lesueuri* Quoy and Gaimard, 1824.

Fig. A. Dorsal aspect in an adult ♂ from Mount Conner, Central Australia. A broad short muzzled phase (X 0.9).

Fig. B. Dorsal aspect in an adult ♂ from the Musgrave Range area of far north-west South Australia. A narrower, longer muzzled phase (X 0.9).

Fig. C. Dorsal aspect in an adult ♂ from River Light, lower South Australia (X 0.8).

Fig. D. Dorsal aspect in an adult ♂ from West Popanyinning, south-west Western Australia (X 0.8).

Fig. E. Palatal aspect of example figured at A (X 0.9).

Fig. F. Lateral aspect of the same (X 0.9).

Fig. G. Occipital aspect of the same (X 0.8).

Fig. H. Lateral aspect of right mandibular ramus of example figured at B (X 1.1).

PLATE XXVIII

Dentition of *Bettongia lesueuri* Quoy and Gaimard, 1824.

Fig. A. Labial and buccal aspects of the upper incisors, canine, P⁴ and MP⁴ in a subadult ♂ from Mount Conner, Central Australia (X 2.9).

Fig. B. The occlusal aspect of same (X 2.9).

Fig. C. Buccal aspect of the lower teeth P₃, MP₃, M₁, M₂ in an immature ♀ from the Musgrave Range area of South Australia (X 3.0).

Fig. D. Occlusal aspect of P₃ and MP₃ of the same (X 3.0).

Fig. E. Buccal aspect of P⁴ in an adult ♂ from the Musgrave Range area (X 2.9).

- Fig. F. Occlusal aspect of the same, showing strong development of the posterointernal (talon) cusp. (X 2.9).
- Fig. G. Occlusal aspect of unworn P^4 in a young adult ♂ from the same locality, showing virtual absence of talon (X 2.8).
- Fig. H. Buccal aspect of P^4 of the same individual (X 3.1).
- Fig. I. Occlusal aspect of the same (X 3.0).
- Fig. J. Occlusal aspect of P^4 in a young adult from Ti-Tree Gully, lower South Australia; a taloned variant with sigmoid outline (X 2.8).
- Fig. K. Buccal aspect of P^4 (of left side) in a young adult ♂ from Popanyinning, south-west Western Australia (X 2.8).
- Fig. L. Occlusal aspect of upper cheek teeth in the immature ♀ figured at C and D, showing unworn crown patterns in M^1 and M^2 (portion of M^3 in alveoli) (X 3.0).
- Fig. M. Occlusal aspect of M^1 - M^4 in an adult ♂ from Mount Conner, Central Australia, showing moderate wear (X 3.0).

PLATE XXIX

The skull in *Bettongia penicillata* subsp.

- Fig. A. Dorsal aspect of an adult ♀ of *B. penicillata ogilbyi* Waterhouse from Augusta, south-west Western Australia (X 0.9).
- Fig. B. Dorsal aspect of a subadult of the same at P^3 - M^2 from Mount Lofty, South Australia (X 1.0).
- Fig. C. Palatal aspect of the example figured at A (X 0.9).
- Fig. D. Lateral aspect of same (X 0.9).
- Fig. E. Occipital aspect of same (X 0.9).
- Fig. F. Lateral aspect of right mandibular ramus of same (X 1.1).
- Fig. G. Dorsal aspect of type skull of *B. penicillata anhydra* (X 0.9).
- Fig. H. Palatal aspect of same (X 0.9).

PLATE XXX

The dentition in *Bettongia penicillata* subsp.

- Fig. A. Labial aspect of upper incisors and canine of the left side in an immature ♂ of *B. penicillata ogilbyi* from Cuballing, south-west Western Australia (X 3.0).
- Fig. B. Occlusal aspect of same (X 3.0).
- Fig. C. Buccal aspect of P^3 and MP^4 in an advanced subadult ♂ in which the molar rows have been completed before the tooth change. Same locality (X 3.1).
- Fig. D. Occlusal aspect of the complete upper series P^3 - M^4 , in the same (X 2.8).
- Fig. E. Buccal aspect of the lower series in the same (X 2.8).
- Fig. F. Occlusal aspect of the same (X 2.8).
- Fig. G. Buccal aspect of P^4 in an adult ♀ of *B. penicillata ogilbyi* from Augusta, south-west Western Australia (X 3.1).
- Fig. H. Occlusal aspect of same (X 3.1).
- Fig. I. Buccal aspect of P^4 in same individual (X 2.9).
- Fig. J. Occlusal aspect of same (X 2.9).
- Fig. K. Buccal aspect of P^4 in the type of *B. penicillata anhydra* (X 2.8).
- Fig. L. Occlusal aspect of P^4 and M^1 - M^4 of the left side of the same (X 2.8).
- Fig. M. Buccal aspect of P^4 in the type of *B. penicillata francisca* (X 3.0).
- Fig. N. Occlusal aspect of P^4 and M^1 - M^4 of the left side of the same (X 3.0).
- Fig. O. Occlusal aspect of P^4 and M^1 - M^4 (right side) in an adult ♂ from lower South Australia, showing considerable wear and a well developed accessory buccal cusp on M^3 (X 2.8).

PLATE XXXI

The characters of the head in *Bettongia penicillata ogilbyi*; an immature ♀ from Cuballing, south-west Western Australia. (Photographed January, 1926.) (X 1.3ca.)

REFERENCES

- Abbie, A. A., 1939: Proc. Zool. Soc. London, 109B, 276.
 Andrews, F. W., 1876: S. Aust. Parl. Paper No. 19.
 Bensley, B. A., 1903: Trans. Linn. Soc., London, 2, IX, 83-217.
 Bolliger, A., 1938: Aust. Medical Review, 1118.
 Boardman, W., 1943: Trans. Linn. Soc., New South Wales, LXVIII, 106.
 ——— 1949: *ibid.* LXXIV, 195.
 Brazenor, C. W., 1950: Mammals of Victoria, Melbourne, 46.
 Browne, J. H., 1897: Trans. Roy. Soc. S. Aust., 72.
 Cabrera, A., 1919: Genera Mamalium; Monotremata, Marsupialia, Madrid, 135.
 Carnegie, D. W., 1898: "Spinifex and Sand", London, 249 *et seq.*
 Collett, R., 1897: Proc. Zool. Soc. London, 317-336.
 Cooper, H. M., 1952: "French Exploration in South Australia", Adelaide, 1-200.
 ——— 1953: "The Unknown Coast", Adelaide, 39.
 Dahl, K., 1897: The Zoologist, 671, 210.
 Finlayson, H. H., 1931: Trans. Roy. Soc. S. Aust., LV, 89.
 ——— 1932: *ibid.* LVI, 148-167.
 ——— 1933: *ibid.* LVII, 201.
 ——— 1935: The Red Centre, Sydney, Map.
 ——— 1936: Trans. Roy. Soc. S. Aust., LX 159.
 ——— 1940: *ibid.* 64. 1. 125-136.
 ——— 1941: *ibid.* 65. 2. 215-232.
 ——— 1957: Ann. Mag. Nat. Hist., 12, X, 552.
 Forbes-Leith and Lucas, 1884: Vict. Nat., 1. 4.
 Gill, Edmund D., 1957: Mémoires. Nat. Mus., Melbourne, 21, 189.
 Gill, Thomas, 1909: Proc. Roy. Geog. Soc. Aust'asia., S. Aust. Branch, X (1907-1908), 181.
 Giles, E., 1889: "Australia twice traversed", London 1, 280.
 Glauert, L., 1933: Jour. Roy. Soc. West. Austr., XIX, 26.
 ——— 1950: *ibid.* XXXIV, 115-134.
 Gould, John, 1840: Proc. Zool. Soc. London, 178.
 ——— 1841: "A monograph of the Macropodidae", London, Pl. XIV.
 ——— 1852: "Mammals of Australia", Pl. LXII and text.
 ——— 1855: *ibid.* Pl. LXIV and text.

- Gray, J. E., 1837: Charlesworth's Mag. Nat. Hist., London, 1, 584.
——— 1843: List Mammals Brit. Museum, London, 94.
- Harper, F., 1945: "Extinct and vanishing mammals of the Old World", New York, 79-81.
- Harvey, J. B., 1840: S. Aust. Magazine, 1, 210.
- Iredale, T., 1937: Aust. Zoologist, 9, 40.
- Johnston, R. M., 1882: Pap. and Proc. Roy. Soc. Tasm., 1881, 12, fig. 64a-c.
- Johnston, T. H., 1943: Trans. Roy. Soc. S. Aust., 67 (2). 263.
- Kreffft, G., 1862: Trans. Phil. Soc. New South Wales, 1.
——— 1864: Cat. Mamms. Aust. Museum, Sydney, 45.
- Le Sonet, A. S., *et al*, 1926: "Wild Animals of Australasia", 236.
- Longman, H. A., 1930: Mems. Queensland Museum, X, 1, 55-64.
- Lundelius, E., 1957: West. Aust. Naturalist, 5, 173-182.
- Lydekker, R., 1894: "Marsupials and Monotremes", Allen's Nat. Library, 68.
- Owen, R., 1866: "Anatomy of Vertebrates", 2. 342.
- Pearson, J., 1947: Reports of A.N.Z.A.A.S. (Adelaide), 1946, 91-93.
——— 1950: Pap. and Proc. Roy. Soc. Tas., 211-229.
- Quoy and Gaimard, 1824: "Voyage Uranie", Zoology, 64.
- Sanger, E. B., 1882: Am. Naturalist., XVIII. 9-14.
- Serventy, D. L., 1953-55: West. Aust. Naturalist, 4, 136.
- Shortridge, G. C., 1910: Proc. Zool. Soc. London 2, 803-848.
- Spencer, B., 1896: "Reports of the work of the Horn Scientific Expedition to Central Australia", Pt. 2. Zoology.
- Tate, R., 1879: Trans. Phil. Soc. S. Aust. (1878-1879), 124.
- Tate, G. H. H., 1948: Bull. Am. Mus. Nat. Hist., 91, 269.
——— 1952: *ibid.* 98, 592.
- Thomas, O., 1888: "Catalogue of Marsupials and Monotremes in the British Museum", 112.
——— 1907: Proc. Zool. Soc. London (1906), 769-773.
- Tindale, N. B., 1940: Trans. Roy. Soc. S. Aust., 64, 1, 142-231, Map.
——— 1957: Rec. S. Austr. Museum, XIII, 1-49.
- Waterhouse, G. R., 1841: Jardine's Naturalists Library, XI, 183.
——— 1842: Proc. Zool. Soc. London, 47.
——— 1846: Natural History of Mammalia, Lond., 1. 203.
- Wood Jones, F., 1923-1925: "Mammals of South Australia", Adelaide, 207.
——— 1923b: Trans. Roy. Soc. S. Aust., XLVII, 94.